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ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

VOLUME 77 BAND



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SOUTH AFRICAN MUSEUM
CAPE TOWN

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VOLUME 77

BAND 77

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Only generic and specific names should be underlined to indicate italics; all other marking up should be left to editor and publisher.

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et al. in text for more than two joint authors, but names of all authors given in list of references.

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FISCHER, P.-H. 1948. Données sur la résistance et de la vitalité des mollusques. *J. Conch.*, Paris 88: 100-140.

FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* 74: 627-634.

KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) 2: 309-320.

KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* 17 (4): 1-51.

THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Sud-Afrika* 4: 269-270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* 16: 269-270.

(continued inside back cover)

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Volume 77 Band
October 1978 Oktober
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THE SOUTH AFRICAN MUSEUM'S
MEIRING NAUDE CRUISES
PART 8
ISOPODA ANTHURIDEA

By
BRIAN KENSLEY

Cape Town Kaapstad

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THE SOUTH AFRICAN MUSEUM'S MEIRING NAUDE CRUISES
PART 8
ISOPODA ANTHURIDEA

By
Brian Kensley
South African Museum, Cape Town

(With 13 figures)

[MS. accepted 21 March 1978]

ABSTRACT

Ten species of anthurid and paranthurid isopods are recorded from deep water off Natal. One is described as a new genus, viz. *Natalanthura foveolata*. A further five species are described as new, viz. *Apanthura insignifica*, *Neohyssura skolops*, *Colanthura uncinata*, *Leptanthura minuta*, and *Leptanthura natalensis*.

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Systematic discussion	2
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INTRODUCTION

The anthuridean isopods were excluded from the report on the isopods of the 1975 and 1976 *Meiring Naude* cruises (Kensley 1977) either for lack of specimens of some species or because of taxonomic uncertainty. With the 1977 cruise more anthurids were collected and some of the taxonomic problems have been resolved. The anthurids of all three cruises are presented here. Station data from the first two cruises may be obtained from Louw (1977), and the South African Museum's unpublished reports and station lists for the 1977 cruise.

SPECIES LIST

	SM Station	♂♂	♀♀	ovig. ♀♀	juvs
Family Anthuridae					
<i>Anthelura remipes</i> Barnard	123	—	1	—	—
	129	—	—	—	1
<i>Apanthura insignifica</i> sp. nov.	123	—	2	—	—
	129	1	3	—	—
<i>Mesanthura catenula</i> (Stimpson)	86	—	1	—	1
<i>Natalanthura foveolata</i> gen. et sp. nov. .	86	—	6	—	—
	123	—	1	—	—
	129	—	—	1	—
<i>Neohyssura skolops</i> sp. nov.	129	—	1	—	—

	SM Station	♂♂	♀♀	ovig. ♀♀	juvs
Family Paranthuridae					
<i>Colanthura uncinata</i> sp. nov. . . .	86	3	—	2	9
	103	13	—	4	12
	78	—	—	1	—
<i>Leptanthura minuta</i> sp. nov. . . .	86	3	2	3	—
	129	2	1	—	—
	53	2	—	—	1
<i>Leptanthura natalensis</i> sp. nov. . . .	60	1	—	—	—
	61	2	—	—	—
	117	1	1	—	—
	123	1	—	—	1
	129	—	7	—	—
	103	—	1	—	—
<i>Paranthura punctata</i> (Stimpson) . . .	103	—	1	—	—
<i>Pseudanthura tenuis</i> Kensley . . .	53	—	1	—	—
	103	—	6	—	—
	129	1	4	—	—

SYSTEMATIC DISCUSSION

Family Anthuridae

Apanthura insignifica sp. nov.

Figs 1-2

Description

Female

Integument thin. Body with following proportions: $C < 1 = 2 = 3 < 4 = 5 > 6 > 7$. Pereonite 7 half length of 6. Pereonites 4 to 7 with faint anterior constriction, pereonite 4 with single, shallow, circular dorsal pit, pereonite 5 with transversely elongate shallow pit, pereonite 6 with two small, shallow pits. Dorsolateral grooves present. Pleonites 1 to 5 completely separate, pleonite 5 slightly longer than preceding pleonites, pleonite 6 with middorsal incision in posterior margin. Telson distally broadly rounded with several setae, widest at about midlength, with low weakly developed middorsal ridge; two large statocysts present at telsonic base. Cephalon with rostrum projecting beyond anterolateral corners; eyes lacking.

Antennular peduncle 4-segmented, basal segment equal to second and third segments together; fourth segment very short, flagellum of two articles bearing three terminal aesthetascs.

Antennal peduncle 5-segmented, two basal segments fairly broad; flagellum of four articles.

Mandibular palp 3-segmented, first and second segments subequal, third segment shorter, with four distal serrate spines; incisor of three teeth, lacinia plate with five teeth; molar process well developed, distally narrowly rounded.

Maxilla elongate, with one strong tooth and five smaller spines distally; inner ramus tipped with single seta.

Lower lip complex tipped with single terminal hook-like lobe on each side.

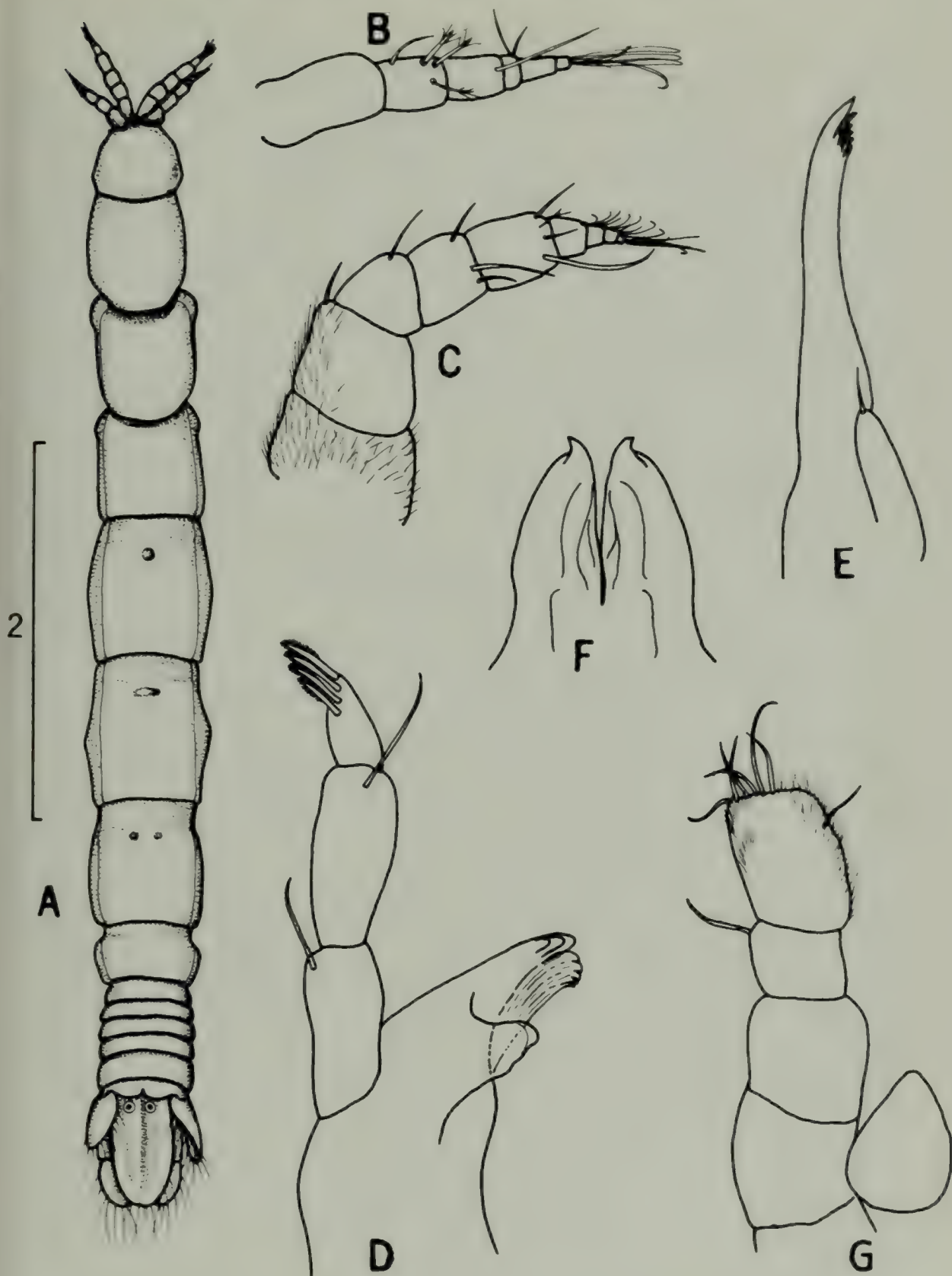


Fig. 1. *Apanthura insignifica*. A. Holotype in dorsal view. B. Antennule. C. Antenna. D. Mandible. E. Maxilla. F. Lower lip complex. G. Maxilliped.

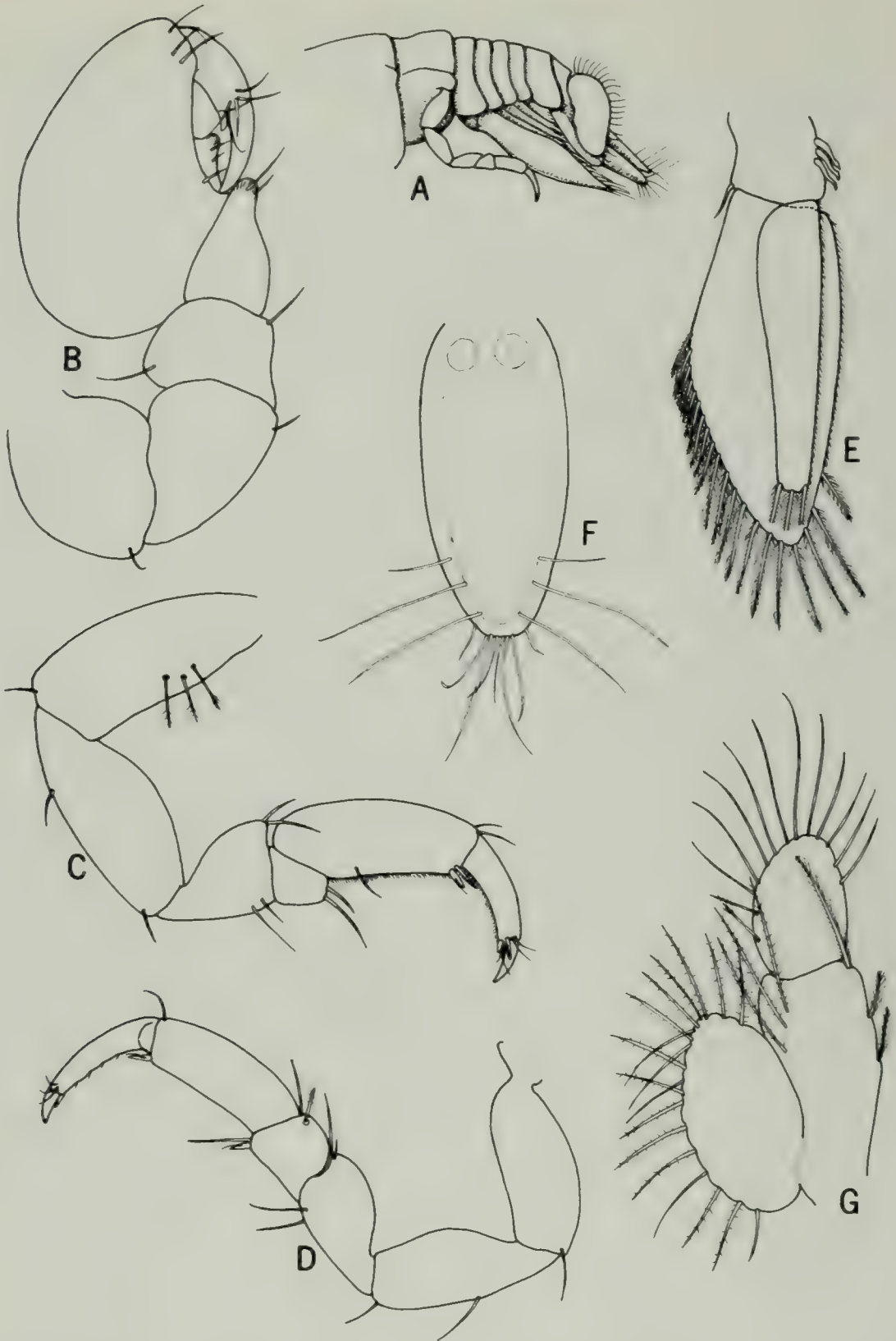


Fig. 2. *Apanthura insignifica*. A. Pereonite 7 and pleon in lateral view. B. Pereopod 1. C. Pereopod 2. D. Pereopod 7. E. Pleopod 1. F. Telson. G. Uropod.

Maxilliped 5-segmented, terminal segment rectangular with several setae on mediiodistal corner.

Pereopod 1 unguis half length of dactylus, with small spine at base; propodus broad, palm concave with strong, rounded lobe at about midpoint; carpus triangular, distally narrowly rounded.

Pereopods 2 to 7 similar, with carpi barely underriding propodi, and becoming slightly more elongate posteriorly.

Pleopod 1 exopod operculate, about three times wider and slightly longer than the endopod, bearing numerous distal plumose setae; endopod with three distal plumose setae; basis with three retinaculae.

Uropodal exopod folding over telson, oval in outline, reaching to end of basis, bearing several sparsely plumose setae; endopod oval, fringed with simple setae.

Submale

Antennular flagellum of about twelve articles extending posteriorly to second pereonite, lacking whorls of aesthetascs.

Pereopod 1 as in female.

Stylet on pleopod 2 not yet detached from endopod.

Material

Holotype SAM-A15646 ♀ TL 5,9 mm SM 123 30°33'S 30°48'E 690 m

Paratype SAM-A15646 1♀ TL 5,2 mm SM 123

Paratypes SAM-A15647 1 sub. ♂ TL 5,6 mm 1♀ TL 4,5 mm SM 129 30°54'S 30°31'E 850 m

Paratypes USNM 170542 2 ♀♀ TL 5,6 mm 5,4 mm SM 129

Remarks

Of the twelve species of *Apanthura* described, only *A. coppingeri* Barnard from the Dundas Straits (northern Australia) and *A. africana* Barnard from South Africa lack eyes. The rhomboid-shaped telson, and the slender uropodal endopod of *A. coppingeri* easily distinguish this species from *A. insignifica*. *A. africana*, known from Saldanha Bay to Still Bay, is a much larger species (up to 20 mm) recorded from shallow water. *A. africana* can further be separated from *A. insignifica* by the maxilliped, which possesses a small terminal segment, and an apically acute telson.

Etymology

The specific name refers to the small size of this species.

Natalanthura gen. nov.

Diagnosis

Integument heavily indurate and very obviously pitted. Mandible with spike-shaped molar on right side, molar reduced to a spine on left side.

Maxilliped 5-segmented with well developed endite. Carpus of pereopods 4 to 7 slightly underriding propodus. Pleopod 1 operculate. Pleonites 1 to 3 subequal, separate; pleonites 4 and 5 fused; pleonite 6 indistinguishably fused with telson. Paired statocysts difficult to detect but probably present beneath two pits at telsonic base.

Type species

Natalanthura foveolata

Etymology

The generic name *Natalanthura* is derived from the South African province of Natal, in whose waters the species was caught, plus the usual 'anthura' suffix. Gender: feminine.

Remarks

The unusual fusion of the pleonites is not encountered in any of the described genera of anthurids. The mandibular structure would also seem to be unique, although reminiscent of *Panathura*. These two features demand the erection of a new genus.

Natalanthura foveolata gen. et sp. nov.

Figs 3-4

Description

Female

Integument indurate and obviously pitted. Anterolateral corners of cephalon extending slightly beyond rostrum. Eyes feebly pigmented, of three or four ocelli. Pereonites with strong dorsolateral ridges and two large dorsal pits per segment in addition to numerous smaller pits. Lateral walls of pereonites pitted. Pereonites 1 to 4 increasing in width and length, pereonite 4 widest and longest; posterior three pereonites decreasing in length, seventh half length of sixth. Pereonites 3 to 5 with oblique dorsal grooves converging anteriorly. Pleon with anterior three pleonites free and distinct; pleonite 4 and 5 fused, line of fusion marked by row of pits; pleonite 6 completely fused with telson. Latter longer than pleonites 1 to 5 combined, distal margin evenly convex, dentate, with strong mediodorsal rounded ridge.

Antennule with broadly curved basal segment plus six additional segments; fourth segment short, terminal segment bearing setae and three or four aesthetascs.

Antenna with 4-segmented peduncle; broad and relatively elongate basal segment with distal triangular part folded over antennule; flagellum of six articles.

Mandible with distal incisor tridentate, quite strongly sclerotized; lacinia plate with row of twelve short teeth; right mandible with digitiform molar

process bearing row of small denticles and striations; molar process reduced to small spine in left mandible; palp 3-segmented, middle segment longest and widest, terminal segment bearing three stout setae.

Maxilla slender and elongate, with four terminal teeth.

Maxilliped 5-segmented, terminal segment rounded, bearing four setae; endite elongate-lanceolate, apically acute, with single seta on median margin, reaching just beyond proximal margin of third segment.

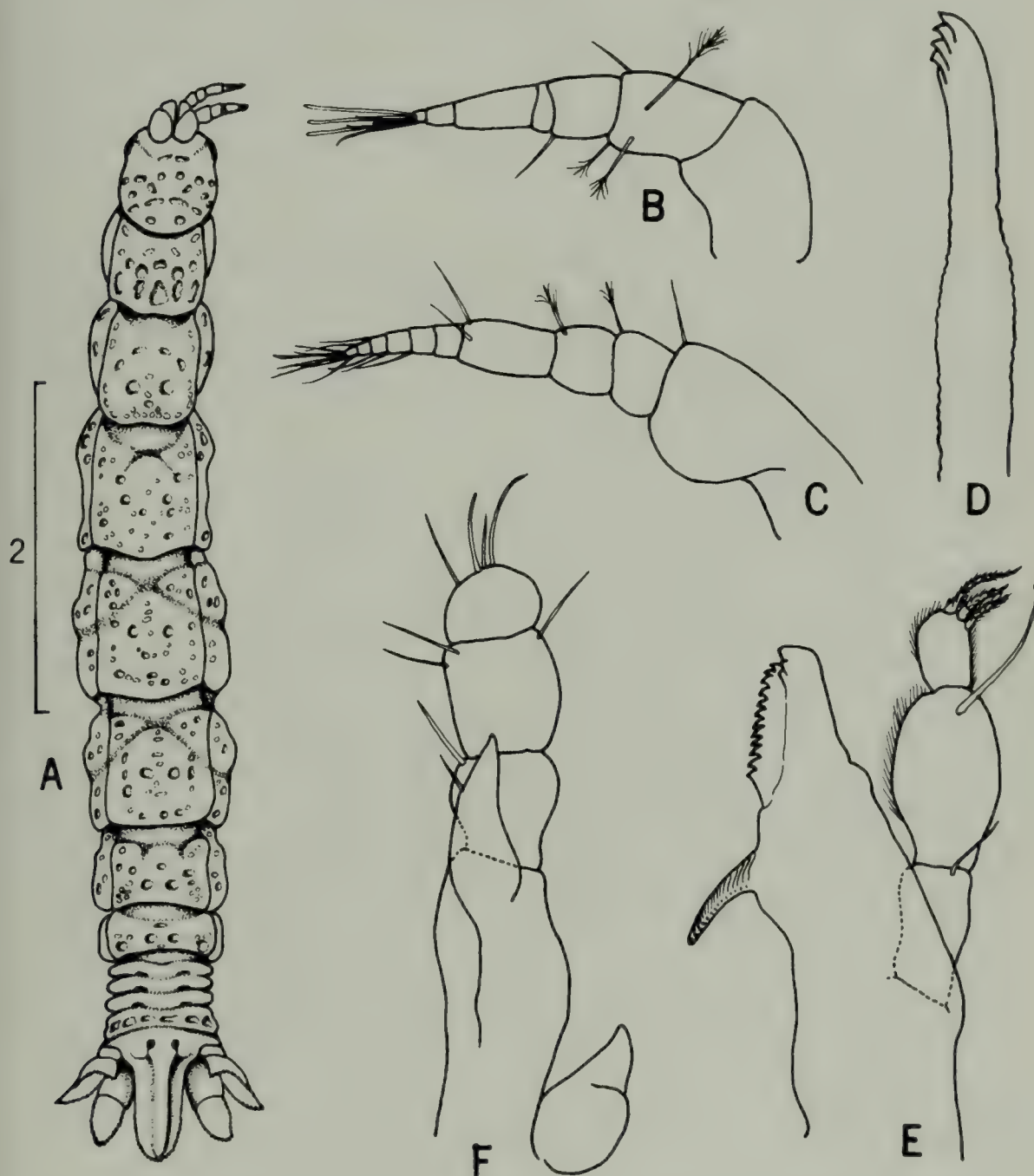


Fig. 3. *Natalanthura foveolata*. A. Holotype in dorsal view. B. Antennule. C. Antenna. D. Maxilla. E. Right mandible. F. Maxilliped.

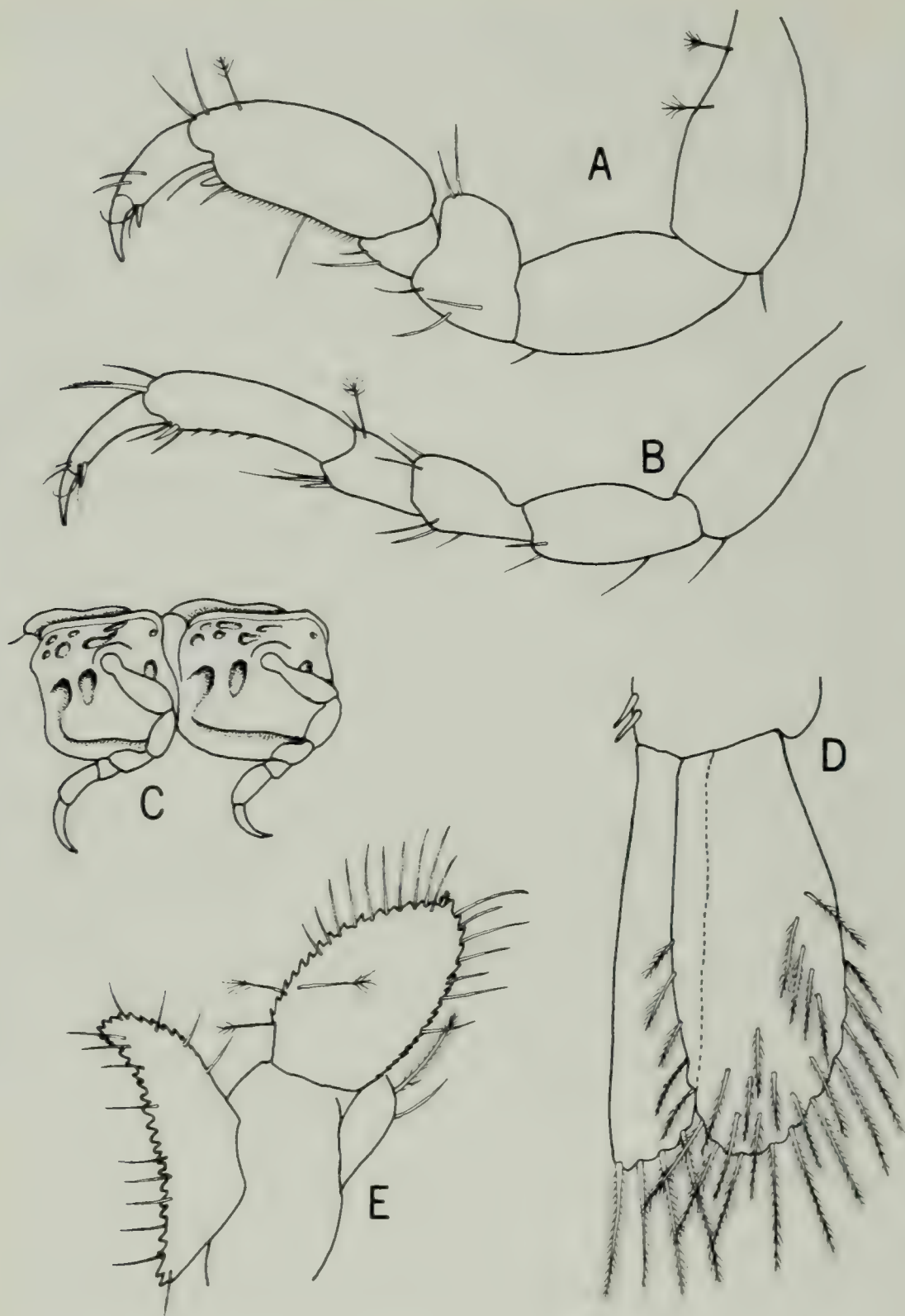


Fig. 4. *Natalanthura foveolata*. A. Pereopod 1. B. Pereopod 7. C. Pereonites 4 and 5 in lateral view. D. Pleopod 1. E. Uropod.

Pereopods 1 and 2 similar, unguis one-third length of dactylus, with single spine at base; propodus with single distal spine and numerous setules on palmar margin. Posterior pereopods with unguis one-third length of dactylus, with short spine at base, propodus with strong distal spine and four or five short, slender spines on ventral margin, and single serrate seta on upper distal margin; carpus about half length of, and slightly underriding, propodus.

Brood pouch formed by four pairs of oostegites.

Pleopod 1 operculate, rami of equal length, endopod half width of exopod, with four distal plumose setae; exopod with numerous plumose setae distally, and with outer surface bearing scales; basis bearing two coupling hooks.

Uropodal endopod subequal to basis in length, entire margin strongly dentate; exopod crescentic and curved, margin strongly dentate; basis triangular in cross-section.

Material

Holotype SAM-A15648 ♀ TL 5,8 mm SM 86 27°59'S 32°40'E 550 m

Paratypes SAM-A15648 2 ♀♀ TL 3,5 mm 5,4 mm SM 86

Paratypes USNM-170543 3 ♀♀ TL 4,3 mm 4,3 mm 4,6 mm SM 86

Paratype SAM-A15649 1 ♀ TL 3,4 mm SM 123 30°33'S 30°48'E 690 m

Paratype SAM-A15650 1 ovig. ♀ TL 6,9 mm SM 129 30°53'S 30°31'E 850 m

Etymology

The specific name refers to the pitted nature of the integument.

Neohyssura skolops sp. nov.

Figs 5–6

Description

Female

Integument thin, only uropods and telson slightly indurate. Body proportions: $C < 1 < 2 = 3 < 4 = 5 = 6 > 7$. Dorsolateral grooves present on pereonites but very difficult to see; dorsal pits absent. Anterior five pleonites separate, equal in length and breadth; pleonite 6 fused with telson; latter with broad, rounded base, tapering rapidly into cylindrical spike-like structure tipped with setae; no statocysts visible. Eyes absent. Anterolateral corner of cephalon extending beyond low rostrum.

Antennular peduncle 4-segmented, two basal segments broad, fourth segment set obliquely into third, short; flagellum of five articles with few setae and single apical aesthetasc.

Antennal peduncle 5-segmented, second and fifth segments subequal, longer than third and fourth segments; second segment grooved to receive antennule; flagellum of seven articles.

Mandibular palp 3-segmented, first and third segments subequal, about one-third length of second segment; incisor of three teeth, lacinia plate bearing five blunt teeth; molar process blunt, tapering.

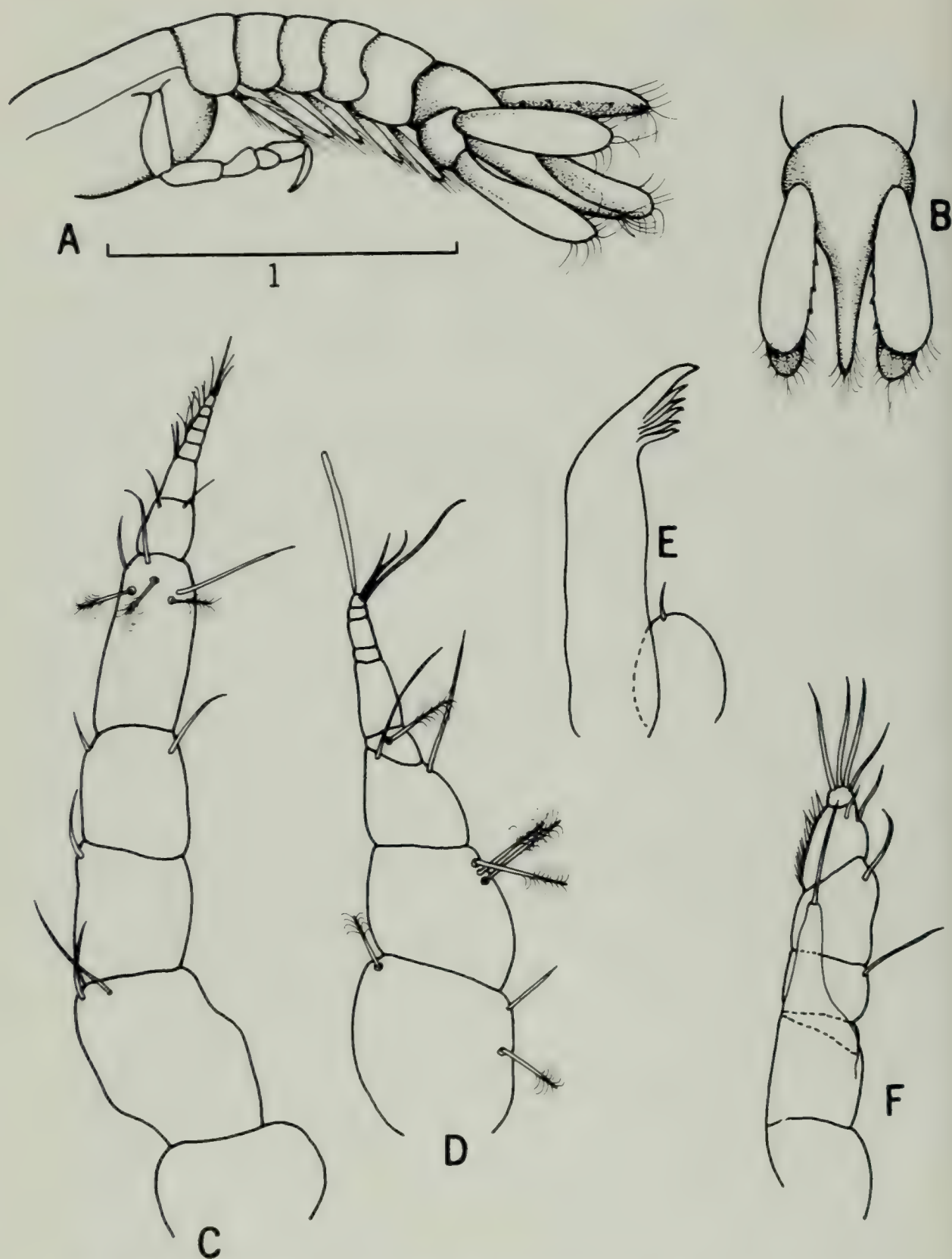


Fig. 5. *Neohyssura skolops*. A. Pereonite 7 and pleon in lateral view. B. Telson and uropods in dorsal view. C. Antenna. D. Antennule. E. Maxilla. F. Maxilliped.

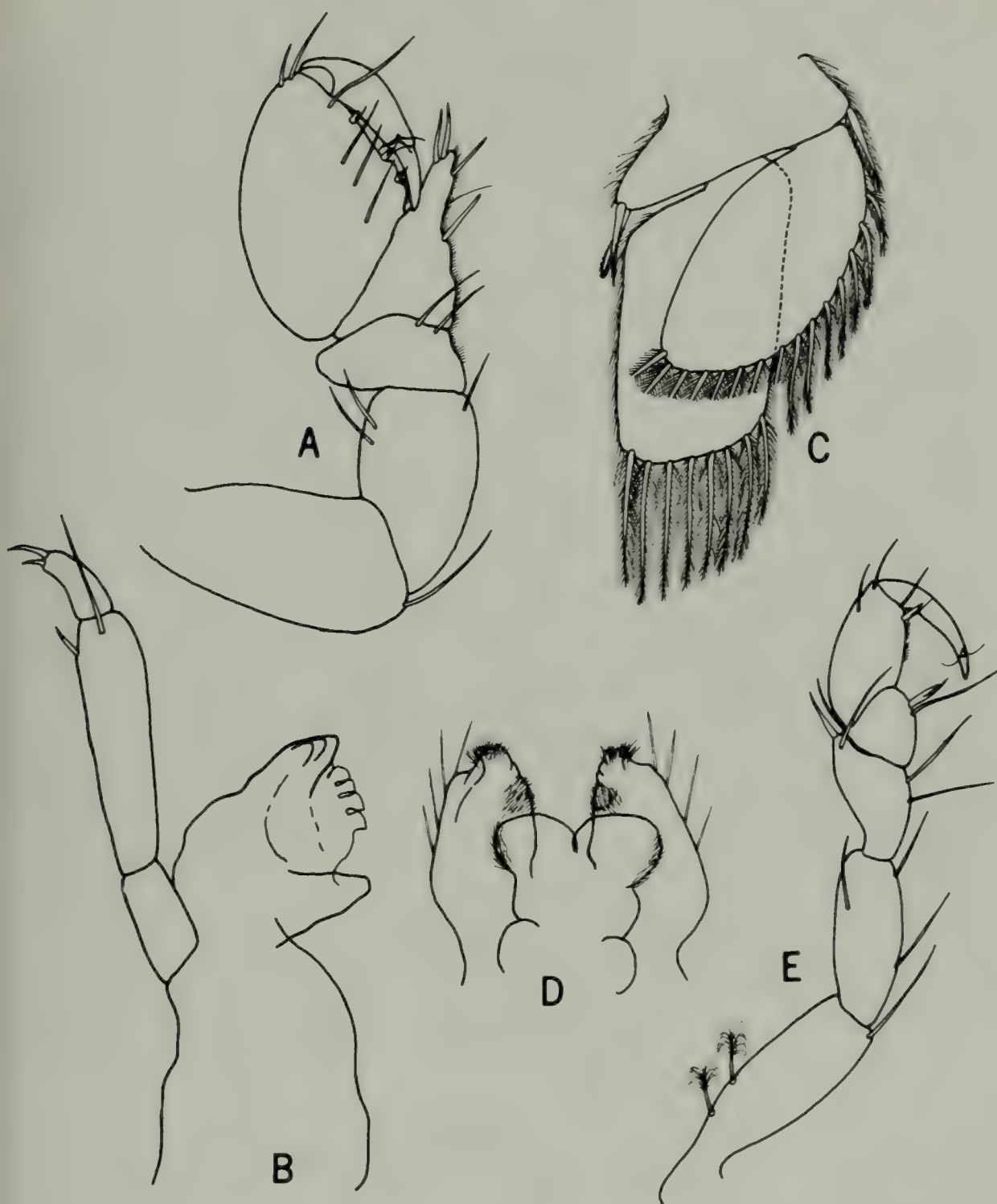


Fig. 6. *Neohyssura skolops*. A. Pereopod 1. B. Mandible. C. Pleopod 1. D. Lower lip complex. E. Pereopod 7.

Maxilla with one strong, outer spine and five smaller spines distally.

Lobes of lower lip distally bearing two short acute processes.

Maxilliped 7-segmented, terminal segment short, bearing four setae; thin-walled endite tapering, with single terminal seta.

Pereopods 1 to 3 similar, subchelate, pereopod 2 more robust than 1 or 3; unguis one-third length of dactylus, propodus proximally broad, palm convex between three short sensory spines, with few scattered setae on inner face; carpus triangular, produced distally well beyond base of propodus to meet dactylus. Pereopods 4 to 7 slender, unguis one-sixth length of dactylus; propodus with strong posterodistal spine; carpus short, underriding propodus, with strong sensory spine on posterior margin.

Uropods somewhat indurate, both rami reaching telsonic apex; exopod situated dorsal to telson, with four strong teeth on medial margin, apically rounded; basis with strong mediodistal spine visible in ventral view.

Material

Holotype SAM-A15651 ♀ TL 5,8 mm SM 129 30°53'S 30°31'E 850 m

Remarks

Barnard (1925) noted that '*Hyssura*' *spinicauda* Walker, 1901, did not fit the generic diagnosis of *Hyssura* but he did not decide on the generic status. Amar (1952), on examining a specimen from Corsica, erected the new genus *Neohyssura* which he defined as follows: close to *Hyssura* but the maxillipeds with seven segments, lacking endite, seventh pereopod present, pereopods 4 to 7 with triangular carpus underriding propodus.

The present specimen agrees with all except one of these characters. The maxilliped does have a thin-walled endite (easily overlooked), but for the rest is very similar to that of *N. spinicauda*. The shape of the telson also differs, being narrowly triangular and bearing lateral spines in *N. spinicauda* but narrowly spike-like in *N. skolops*. (See Walker 1901, pl. 27, figs 7-11; Monod 1925, pl. 44.)

Etymology

The specific name '*skolops*' is taken from the Greek word meaning a sharp object such as spike, and refers to the shape of the telson.

Family **Paranthuridae**

***Colanthura uncinata* sp. nov.**

Figs 7-8

Description

Male

Entire integument covered with small imbricate scales. Rostrum extending slightly beyond anterolateral corners of cephalon. Eyes ovate, lateral, consisting of fourteen ocelli. Cephalon two-thirds length of pereonite 1. Pereonites 1 to 5

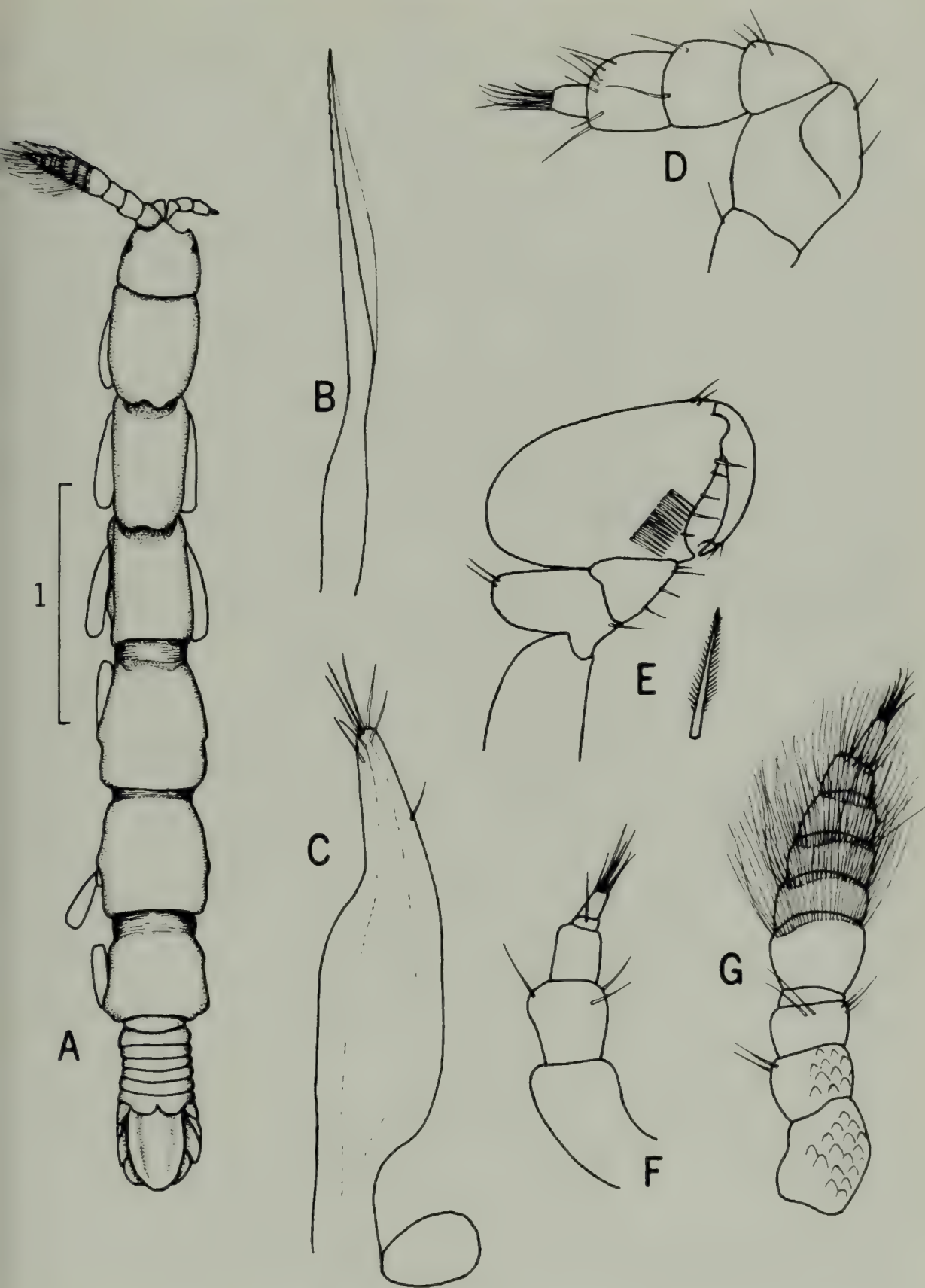


Fig. 7. *Colanthura uncinata*. A. Holotype in dorsal view. B. Maxilla. C. Maxilliped. D. Antenna. E. Pereopod 1 with spine further enlarged. F. Antennule ♀. G. Antennule ♂.

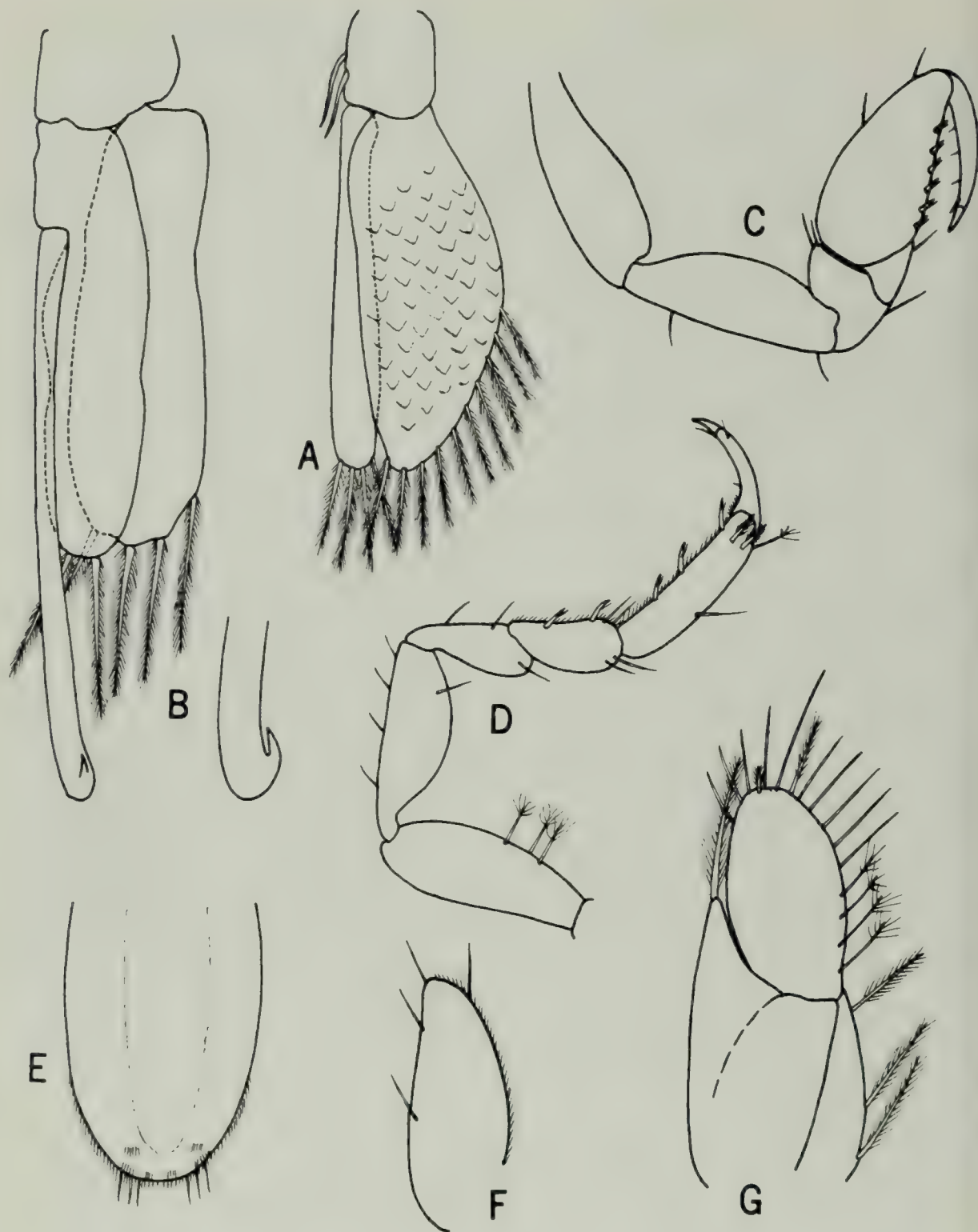


Fig. 8. *Colanthura uncinata*. A. Pleopod 1. B. Pleopod 2 ♂ with apex of stylet further enlarged. C. Pereopod 2. D. Pereopod 6. E. Telson. F. Uropodal exopod. G. Uropodal endopod and basis.

increasing in width, but subequal in length; posterior margins of pereonites 1 and 2 bilobed. Pereonite 6 two-thirds length of pereonite 5; pereonite 7 very short, subequal to anterior pleonites in length and width, lacking pereopods. Ventral surface of pereonites formed by two longitudinal, low, rounded ridges, conspicuously scaled. Pleon narrower than pereon; pleonites 1 to 5 subequal, pleonite 6 posteriorly bilobed, almost twice length of preceding pleonite. Telson equal to pleonites 1 to 6 in length, distally evenly convex; dorsally with low, rounded median area widest proximally.

Antennular peduncle 4-segmented, basal segment largest; flagellum of six articles, five proximal articles broad, bearing dense aesthetascs, terminal article narrow, bearing setae.

Antennal peduncle 5-segmented, second segment largest and broadest; flagellum reduced to setiferous terminal article about one-third width and half length of penultimate segment.

Mandible reduced to blunt lobe lacking palp.

Maxilla very slender, acute, with about ten faint distal serrations.

Maxilliped elongate, consisting of a single segment, distally narrowed, with about seven terminal setae.

Pereopod 1 dactylus strongly curved, unguis short; propodus broadly oval, palm gently sinuous, with triangular proximal process and row of fourteen fringed spines set back from the triangular process.

Pereopod 2 dactylus gently curved, unguis short; propodus proximally broad, distally narrowed, palm with short spines.

Pereopods 3 to 7 similar, unguis of dactylus relatively longer than in pereopods 1 and 2; propodus with three spines and numerous fine setules on ventral margin, plus two distal fringed spines; carpus not underriding propodus, bearing two ventral spines.

Pleopod 1 exopod broad and operculate, with scales on external face; endopod as long as, but one-third width of, exopod.

Pleopod 2 exopod and endopod subequal in length and width, each with few distal plumose setae; stylet of endopod extending well beyond apices of rami, distally rounded with strong subapical hook.

Uropodal endopod just extending to telsonic apex, oval; exopod narrowly ovate, apically narrowly rounded.

Ovigerous female

Antennule consisting of five segments, penultimate segment very short.

Pereopod 1 similar to that of male, but with spine row of six (rather than fourteen) spines. Brood pouch formed by four pairs of oostegites, containing four eggs or four larvae.

Material

Holotype SAM-A15652 ♂ TL 3,9 mm SM 103 28°31'S 32°34'E 680 m

Allotype SAM-A15652 ovig. ♀ TL 4,5 mm SM 103

Paratypes USNM 170544 2 ♂♂ 1 ovig. ♀ SM 103
 10 ♂♂ 2 ovig. ♀♀ 12 immature SM 103
 Paratypes SAM-A15653 2 ♂♂ 1 ovig. ♀ SM 86 27°59'S 32°40'E 550 m
 1 ♂ 1 ovig. ♀ 9 immature SM 86

Remarks

Four species of *Colanthura* have been described. These are *C. tenuis* Richardson, 1902, from Bermuda; *C. squamosissima* Menzies, 1951, from California; *C. nigra* Nunomura, 1975, from Japan, and *C. caeca* Mezhev, 1976, from Russia. The present material most closely resembles the Californian species, this similarity being most marked in the character of the integument, both species being almost covered with imbricate scales. Several differences between these two species are apparent. These include pleonites 1 to 5, which in *C. uncinata* are subequal, while in *C. squamosissima* pleonite 5 is four times the length of the preceding segment; the telson, which is more obviously tapered in *C. uncinata*; and the apex of the stylet of pleopod 2 ♂, which has a swollen apical lobe in Menzies's species, but is hooked in *C. uncinata*. The stylet of pleopod 2 ♂ in *C. caeca* is also apically hooked, but possesses three smaller supplementary apical spines (Mezhov 1976, fig. 3). The shape of the uropodal exopod and telson, and the propodal spination of the pereopods of the Russian species differs from *C. uncinata*.

Etymology

The specific name is taken from the hooked stylet of pleopod 2 ♂.

Leptanthura minuta sp. nov.

Figs 9-10

Description

Male

Body slender, elongate, not indurate. No dorsal pits or dorsolateral grooves present. Cephalon subequal to pereonite 1 in length; eyes lacking. Body proportions: C=1<2=3=4<5>6>7. Pleon equal to pereonites 6 and 7 together in length; all pleonites distinct, pleonites 1 and 5 slightly longer than 2 to 4; pleonite 6 with convex distal margin. Telson elongate-oval in outline, distally evenly rounded, with four median setae; ventrally concave; dorsally with gently raised central area; prominent statocyst present with single medio-dorsal pore.

Antennule with 4-segmented peduncle, basal segment largest, fourth segment very narrow; flagellum of eight articles each with dense whorl of aesthetascs.

Antenna with 5-segmented peduncle, second segment longest, with disto-dorsal triangular part folding over basal antennular segment; flagellum of four articles.

Mandible narrowly triangular, apically acute; 3-segmented palp with middle segment two and a half times length of basal segment, terminal segment short and curved, with single terminal seta.

Maxilla lanceolate, apically acute, with about twelve faint distal serrations.

Maxilliped 3-segmented, with few distal setae; second segment six times longer than wide.

Pereopod 1 dactylus fairly stout, unguis one-third length of rest of segment; propodus proximally broad, palm straight with low triangular proximal

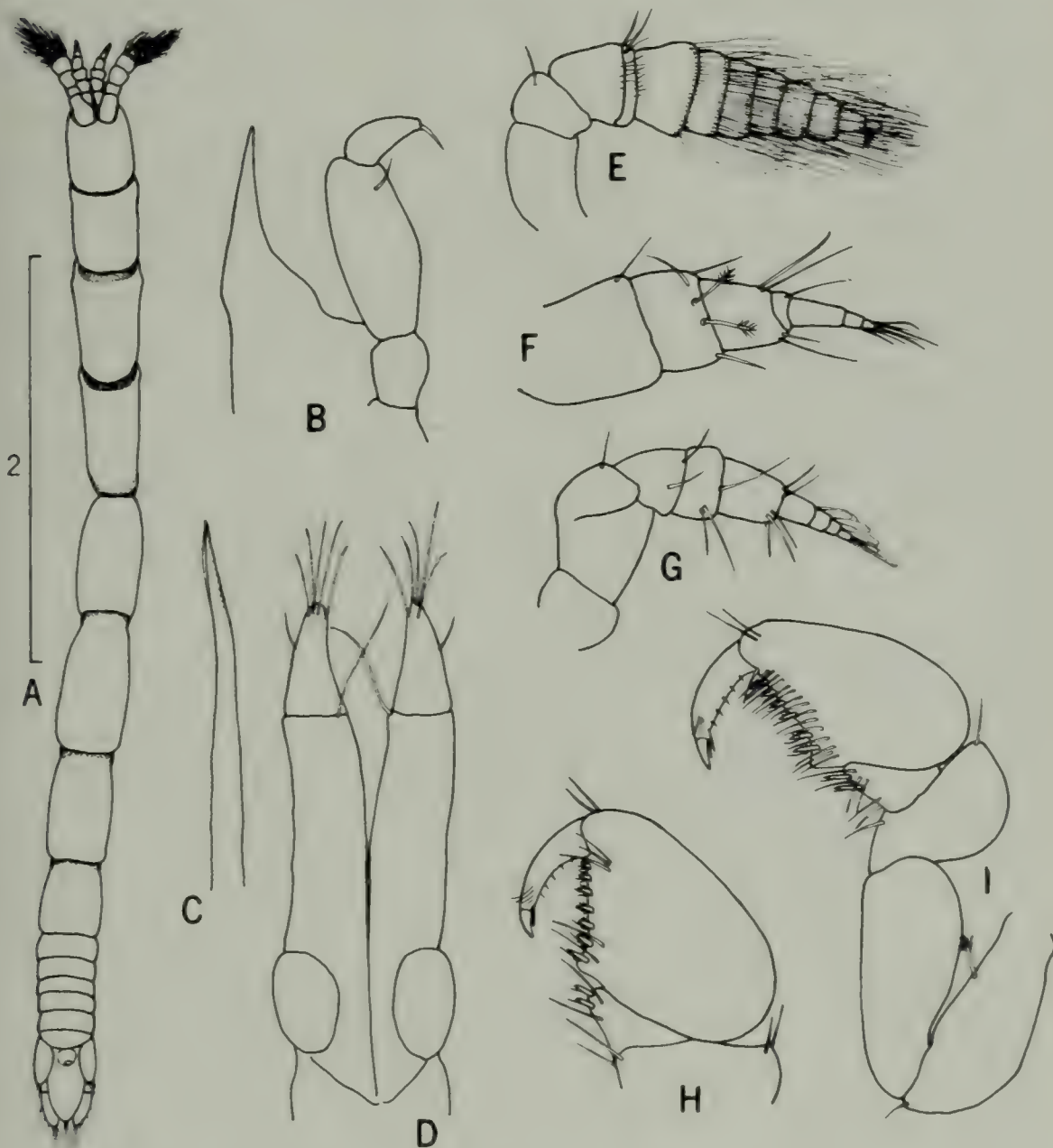


Fig. 9. *Leptanthura minuta*. A. Holotype in dorsal view. B. Mandible. C. Maxilla. D. Maxilliped. E. Antennule ♂. F. Antennule ♀. G. Antenna. H. Pereopod 1 ♀. I. Pereopod 1 ♂.

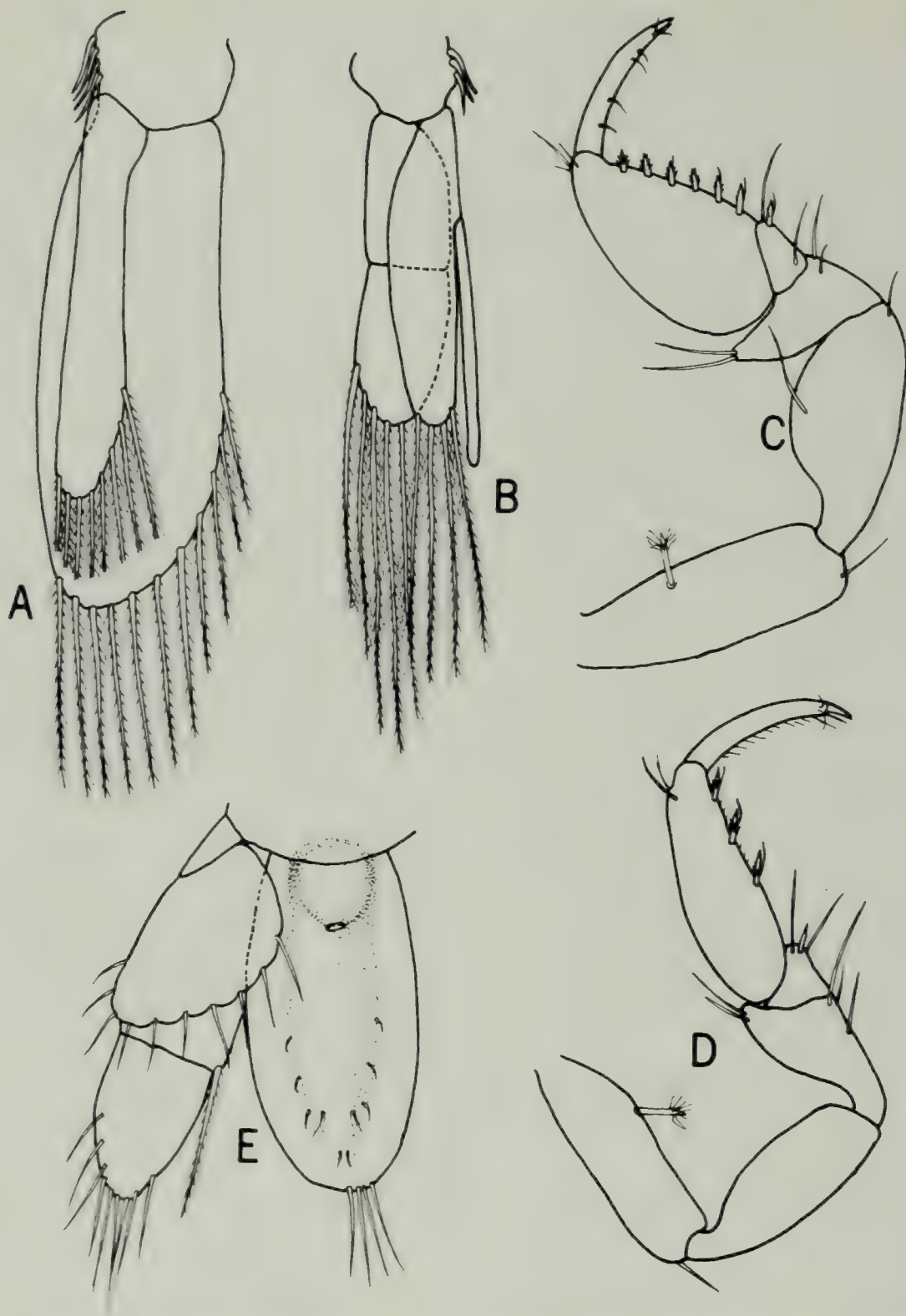


Fig. 10. *Leptanthura minuta*. A. Pleopod 1. B. Pleopod 2 ♂. C. Pereopod 2. D. Pereopod 7. E. Telson and uropod.

tooth, armed with six short serrate spines and numerous simple setae; carpus triangular, small, with two spines and four setae on ventral margin.

Pereopod 2 slightly less robust than pereopod 1, propodus with six spines on palm, lacking dense setae found on pereopod 1; carpus with single ventral spine. Pereopods 4 to 7 similar, slender; propodi with three serrate spines on ventral margin; carpus short, triangular, underriding propodus, with single ventral spine.

Pleopod 1 basis with four retinaculæ on median margin, exopod operculate, two and a half times longer than broad with about ten to twelve distal elongate plumose setae; endopod one-third width and two-thirds length of exopod, with eight distal plumose setae.

Pleopod 2 with three or four retinaculæ on basis; rami subequal in length; exopod with transverse articulation at midlength and about eight distal plumose setae; endopod with four distal plumose setae, stylet on median margin extending well beyond apex of ramus, apically blunt.

Uropodal exopod extending to base of endopod, triangular-oval, median margin crenulate and setose; basis with single elongate plumose seta at medio-distal angle; endopod with several distal setae, apically rounded.

Female

Antennule with 4-segmented peduncle, basal segment longest and broadest, fourth segment very narrow; flagellum reduced, consisting of three articles.

Pereopod 1 very similar to pereopod 1 ♂, but lacking numerous simple setae on palm.

Brood pouch of four pairs of oostegites, anterior pair smallest.

Material

Holotype	SAM-A15654	♂	TL 4,6 mm	SM 86	27°59'S	32°40'E	550 m
Allotype	SAM-A15654	ovig. ♀	TL 4,5 mm	SM 86			
Paratypes	SAM-A15654	1 ♂ 1 ovig. ♀ 1 ♀		SM 86			
Paratypes	USNM 170545	1 ♂ 1 ovig. ♀ 1 ♀		SM 86			
	SAM-A15655	1 ovig. ♀		SM 78	27°31'S	32°50'E	750 m
	SAM-A15656	2 ♂♂ 1 ♀		SM 129	30°53'S	30°31'E	850 m

Remarks

The present small blind species with its characteristic elongate-oval telson and crenulate uropodal exopod bears no close resemblance to any of the approximately eighteen described species of *Leptanthura*. Certainly it is very different from the described South African species, viz. *L. agulhasensis*, *L. laevigata*, and *L. urospinosa*. The shape of the telson of *L. minuta* to some extent resembles that of *L. antarctica* Kussakin, 1967, but the shape of the uropodal endopod and exopod, the antennular peduncle, and the first pereopod easily separate these species.

Etymology

The specific name derives from the small size of the adult animals.

Leptanthura natalensis sp. nov.

Figs 11–12

*Description**Male*

Body very slender and elongate. No dorsal pits. No dorsolateral grooves present, but dorsolateral ridge developed on cephalon and pereonites 1 and 2. Cephalon lacking eyes. Body proportions: $1 < 2 < 3 < 4 > 5 > 6 > 7$. Pereonite 5 in small males (6–7 mm) with two rounded posteroventral lobes; holotype male (20,6 mm) with similar lobes on pereonite 7. Pleonites free. Telson distally broadly rounded, not indurated, dorsally slightly concave, with single, large proximal statocyst.

Antennule with 4-segmented peduncle, basal segment largest, fourth segment short; flagellum of thirteen articles.

Antenna 8- or 9-segmented, of which three distal segments are probably flagellum; second segment longest.

Mandible acutely triangular, palp 3-segmented, basal segment two-thirds length of middle segment, latter with single elongate distal seta, terminal segment short and curved.

Maxilla slender, with twelve serrations and three barbs distally.

Maxilliped 4-segmented, second segment four and a half times longer than wide, with short distal lobe bearing two setae at mediiodistal angle; two distal segments narrowing, bearing few setae.

Pereopod 1 dactylus with very short unguis; palm of propodus almost straight, with low proximal triangular lobe, and row of fourteen short sensory spines, several elongate setae, and dense border of short simple setae.

Pereopod 2 propodus narrower than that of pereopod 1, with nine or ten sensory spines on palm, lacking dense border of simple setae; carpus small, triangular, with two spines on ventral margin.

Pereopod 7 with short carpus bearing two spines and underriding propodus; latter with three spines on ventral margin.

Pleopod 1 operculate, not indurated; endopod considerably shorter than exopod, both rami bearing distal plumose setae; basis bearing about six retinaculae on medial margin.

Pleopod 2 endopod shorter than exopod, with apically blunt stylet on medial margin; exopod with distinct transverse articulation at about midlength, both rami with distal plumose setae; basis armed with five or six retinaculae on medial margin.

Uropodal basis triangular in cross-section, longer than endopod; latter narrower than basis, with tuft of apical setae; exopod broadly oval, with few marginal setae, exopods overlapping telson dorsally.

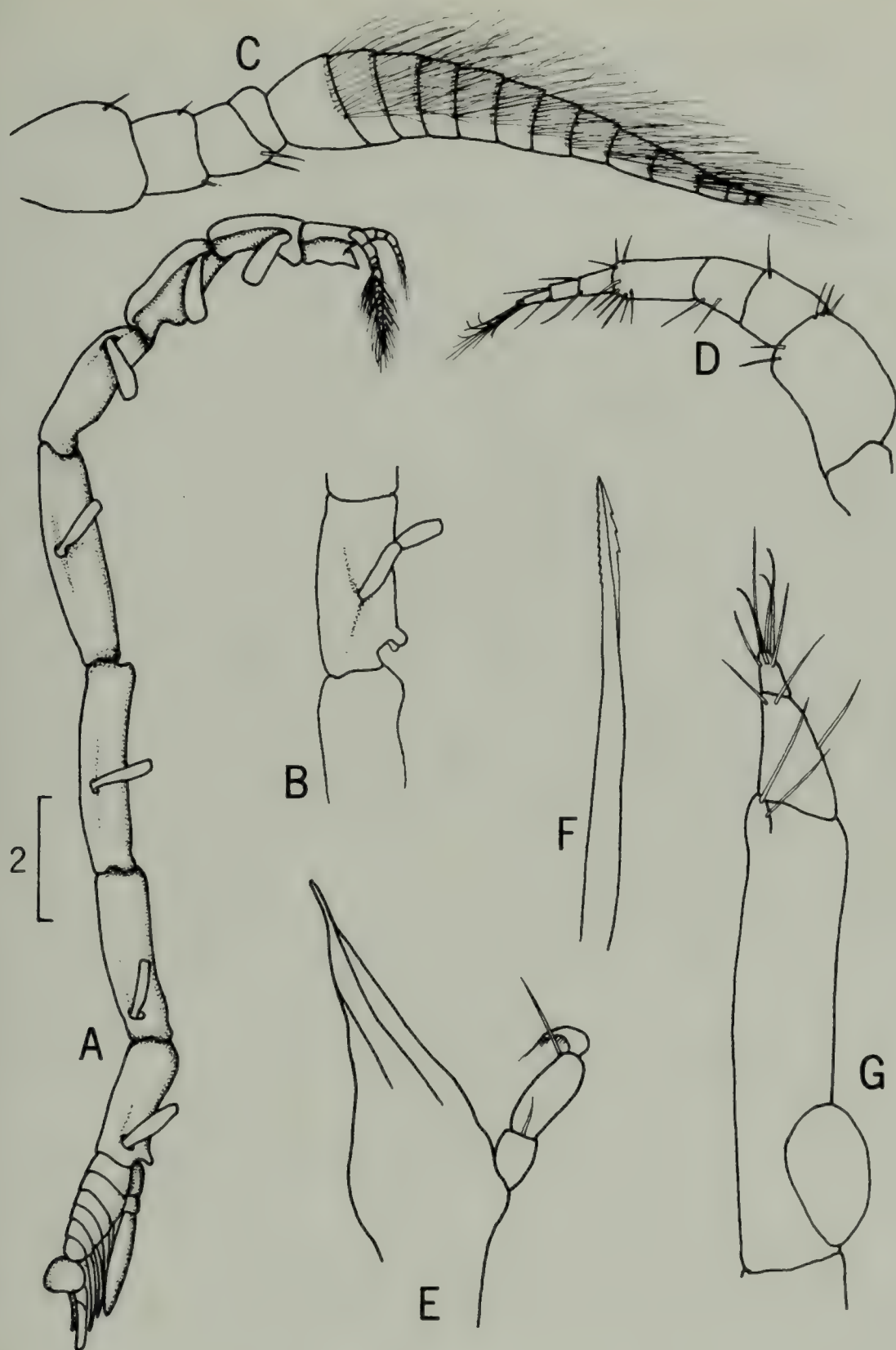


Fig. 11. *Leptanthura natalensis*. A. Holotype in lateral view. B. Pereonite 5 of 6,8 mm ♂. C. Antennule ♂. D. Antenna. E. Mandible. F. Maxilla. G. Maxilliped.

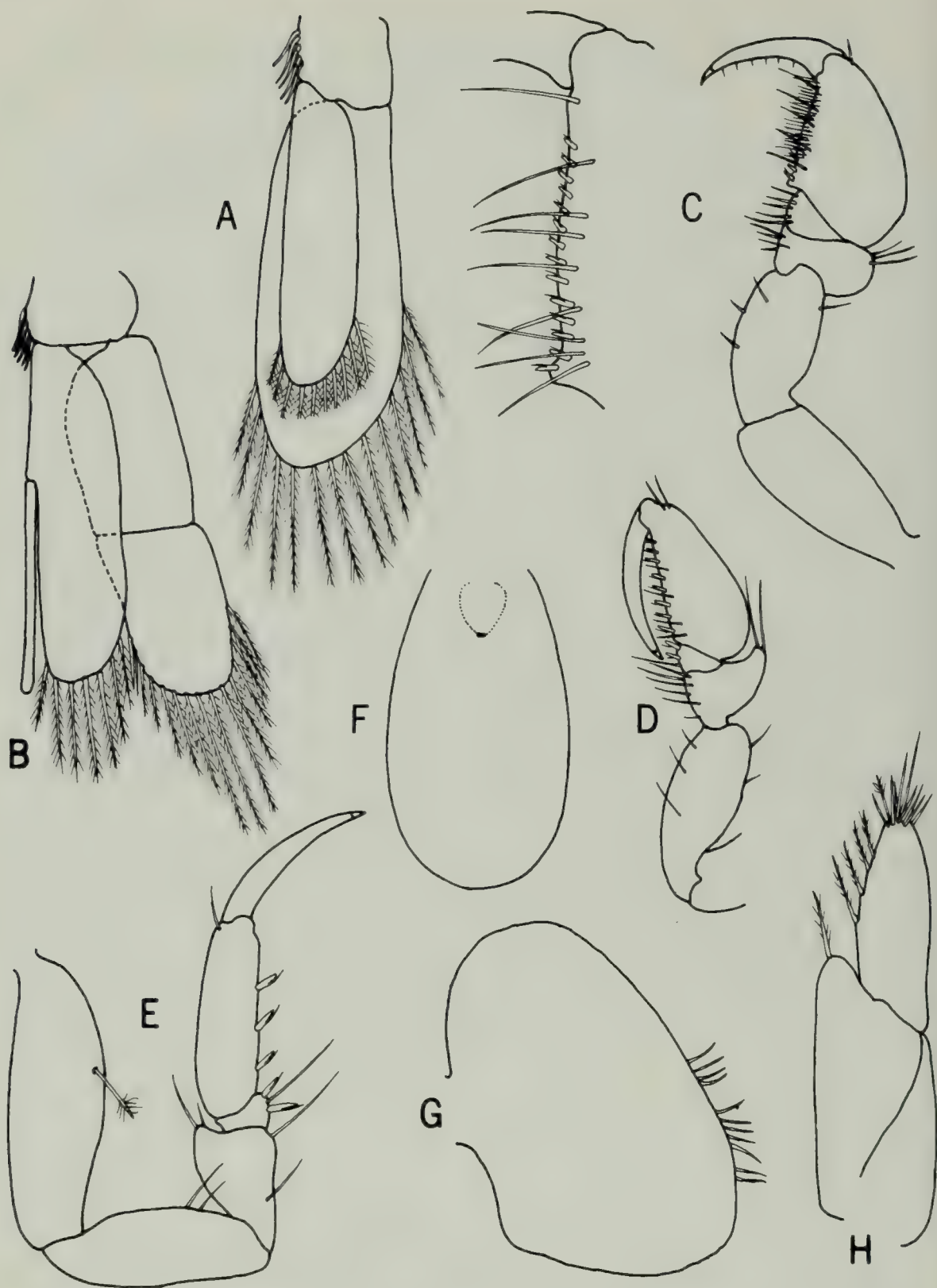


Fig. 12. *Leptanthura natalensis*. A. Pleopod 1. B. Pleopod 2 ♂. C. Pereopod 1 ♂, with palm enlarged (short, simple setae omitted). D. Pereopod 2. E. Pereopod 7. F. Telson. G. Uropodal exopod. H. Uropodal basis and endopod.

Material

Holotype	SAM-A15657	♂	TL 20,6 mm	SM 60	27°09'S 32°58'E	800 m
Paratypes	SAM-A15658	2 ♂♂	TL 6,8 mm	6,7 mm	1 juv. 4,8 mm	
				SM 53	26°51'S 33°12'E	720 m
Paratypes	SAM-A15659	2 ♂♂	TL 6,7 mm	7,5 mm	SM 61	27°10'S
					32°58'E	820 m
Paratypes	USNM 170546	1 ♂	TL 8,0 mm	1 ♀ 5,7 mm	SM 117	30°17'S
					31°10'E	820 m
	SAM-A15660	1 ♂	9,9 mm	1 juv.	SM 123	30°33'S 30°48'E
					690 m	
	SAM-A15661	7 ♀♀	complete but damaged			SM 129 30°53'S
						30°31'E 850 m

Remarks

The general structure of the pereon and pleon, as well as the mandible, maxilliped, antennae, and pereopods of the present material, agrees with *Leptanthura*, and quite closely resembles *L. laevigata* and *L. glacialis*. The broadly rounded telson is similar to that of *L. laevigata* (Stimpson) (Barnard 1925), but *L. natalensis* lacks the characteristic notch in the uropodal exopod, and is a more attenuated species both in body shape and pereopodal proportions. The terminal maxillipedal segment is longer than that of *L. laevigata*. *L. glacialis* Hodgson (Kussakin 1967) has a uropodal exopod similar to *L. natalensis* but possesses an apically pointed telson, and shorter and broader antennal segments. *L. glacialis* appears to have a 3-segmented maxilliped, rather than the 4-segmented structure of *L. natalensis*.

Etymology

The specific name is taken from the province, Natal, from whose waters the species was taken.

Pseudanthura tenuis Kensley

Fig. 13

Pseudanthura tenuis Kensley, 1978: 222, figs 1-2.

*Description**Male*

Antennular peduncle 4-segmented; segments broad, basal segment equal in length to three distal segments combined; basal flagellar article broad and almost as long as remaining seven flagellar articles together; six distal articles each with pair of aesthetascs.

Pleopod 2 stylet of endopod extending well beyond apex of ramus, straight, apically rounded.

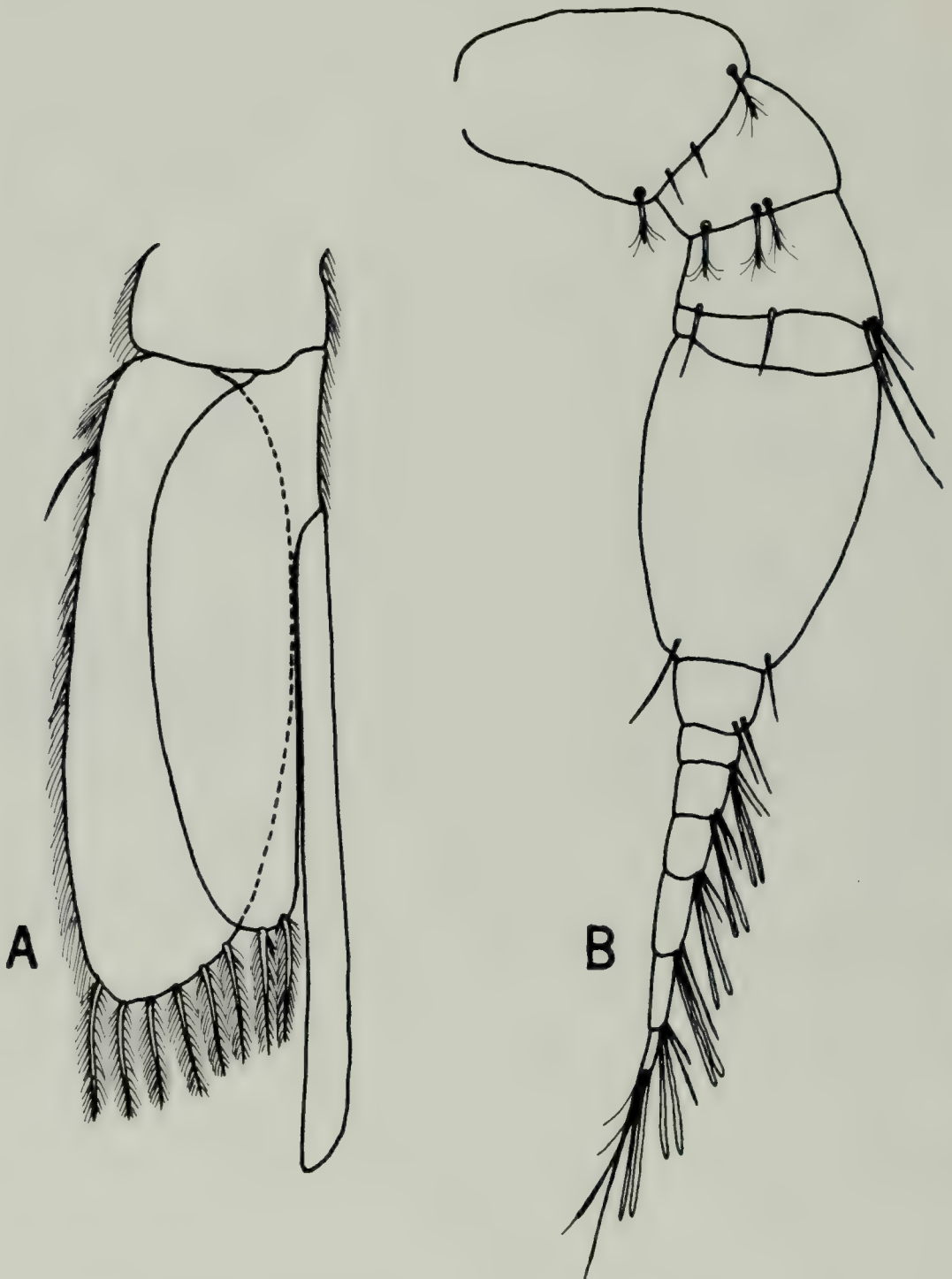


Fig. 13. *Pseudanthura tenuis*. A. Pleopod 2 ♂. B. Antennule ♂.

Material

1 ♀ TL 9,9 mm SM 53 26°51'S 33°12'E 720 m
 6 ♀♀ TL 6,0–25,3 mm SM 103 28°31'S 32°34'E 680 m
 1 ♂ TL 20,7 mm SM 129 30°53'S 30°31'E 850 m

Remarks

P. tenuis Kensley was described from seven females from localities very close to that of the present material. Now that a single male is available, the two main sex-linked characters are described and figured.

ACKNOWLEDGEMENTS

In addition to the people and institutions thanked in the introductory paper in this series, I should like to thank Mr R. Downes of the South African Museum for sorting the samples of the 1977 cruise. My sincere thanks are also due to Dr T. E. Bowman of the Smithsonian Institution for useful discussions and for critically reading the manuscript.

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Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierii Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

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In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as

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Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

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(continued inside back cover)

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ADDITIONS TO THE REVISED LIST OF PRESERVED
MATERIAL OF THE EXTINCT CAPE COLONY
QUAGGA AND NOTES ON THE RELATIONSHIP AND
DISTRIBUTION OF SOUTHERN PLAINS ZEBRAS

By
R. E. RAU

Cape Town Kaapstad

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ADDITIONS TO THE REVISED LIST OF PRESERVED MATERIAL
OF THE EXTINCT CAPE COLONY QUAGGA
AND NOTES ON THE RELATIONSHIP AND DISTRIBUTION OF
SOUTHERN PLAINS ZEBRAS

By

R. E. RAU

South African Museum, Cape Town

(With 9 figures)

[MS. accepted 7 September 1978]

ABSTRACT

Previously unpublished photographs and data of two mounted skins of the extinct quagga (*Equus quagga quagga*) and a further relic are added to the list of preserved material. Photographs of the destroyed Königsberg quagga are reproduced.

Examination of plains zebra (*Equus 'burchelli'*) skins from southern Africa and comparison with the true Burchell's zebra (*Equus 'burchelli burchelli'*) and the quagga (*Equus quagga quagga*) suggest that all belong to one species (*Equus quagga*) and are forms which are dominant in certain areas within the continuous distribution, rather than subspecies. In addition, the true Burchell's zebra is considered to be still extant in Zululand and possibly Swaziland, if the generally accepted but vague range of that 'subspecies' is ignored.

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INTRODUCTION

Since the publication of the revised list of preserved material of the quagga (*Equus quagga quagga*) a photograph of and additional data on the quagga at the Zoological Museum, State University at Kazan, Soviet Union, have now been obtained. In addition, a mounted quagga has been discovered at the Muséum d'Histoire Naturelle Lyon, France, and a mounted foot at the Royal Albert Memorial Museum at Exeter, England. These new data are presented in accordance with the method followed by Rau (1974). The photographs included in the description of the Königsberg quagga (Hilzheimer 1930), which was destroyed at the end of the Second World War, are reproduced to complete the illustrations of mounted skins which existed into this century.

In a monograph Antonius (1951), a world authority on zebras, included the quagga and the Burchell's zebras in the single species *Equus quagga*, as had been done earlier (Pocock 1904; St Leger 1932). This view is supported by Rzasnicki (1951), Mohr (1964) and Klingel (1969, 1972) amongst others. There is, however, a second school of thought which divides them into two species, *Equus quagga* and *Equus burchelli* (Ansell 1971). As the present study has revealed that there is no definite division between the quagga and Burchell's zebras, the former view is supported.

ADDITIONAL MATERIAL

KAZAN—MOUNTED SKIN

Fig. 1

Catalogue number: 109

Sex: female

Locality: unknown

Date of acquisition: 1843

Remarks on acquisition: bought in Hamburg from a Mr Brandt by Professor Eversman for the Zoological Museum of Kazan University



Fig. 1. Kazan quagga.

History of mount: bought as mounted specimen in bad condition and remounted; a second remounting ('restoring') was performed in 1969 by M. A. Zaslavski in Leningrad, U.S.S.R.

Description of striking features: face clearly striped; shadow-stripes on neck; posterior part of feet (fetlock-hoof) dark; the photograph seems to show faint striping on buttock

<i>Measurements:</i> head-body	2,36 m*	(2,42 m)*
tail	0,54 m	(0,53 m)
ear	0,14 m	(0,17 m)
hind foot	0,56 m	(0,54 m)
shoulder height	1,29 m	(1,28 m)

State of preservation: appears to be good

Further material of same individual: none

Remarks: exhibited open in gallery

References: none known

LYON—MOUNTED SKIN

Fig. 2

Catalogue number: 6102

Sex: female

Locality: Kaffraria, South Africa

Date of acquisition: unknown

Remarks on acquisition: none

History of mount: appears to be the original mount

Description of striking features: face not clearly striped

<i>Measurements:</i> head-body	2,10 m
tail	0,40 m
ear	0,17 m
hind foot	0,50 m
shoulder height	1,15 m

State of preservation: fair

Further material of same individual: none

Remarks: exhibited; specimen not mentioned in previous literature; V. Eisenmann of the Muséum d'Histoire Naturelle, Paris, discovered this specimen early in 1975 and kindly informed the author

References: M. Philippe, 'La zoologie au Muséum d'Histoire Naturelle de Lyon' (in preparation)

* Measurements received through two intermediaries are not identical.



Fig. 2. Lyon quagga.

EXETER—FOOT TROPHY

Fig. 3

Catalogue number: A758

Locality: Bontebok Flats, British Kaffraria, South Africa (between present Cathcart and Queenstown)

Date of acquisition: after 1869

Remarks on acquisition: from the collection of W. S. M. D'Urban, first curator of Exeter Museum

Measurements (hoof only):

anterior height	6,0 cm
width	6,7 cm
length	8,4 cm

References: Howes & Bamber (1970)



Fig. 3. Exeter quagga foot; anterior and lateral views.

KÖNIGSBERG QUAGGA

Fig. 4

The Königsberg quagga was destroyed at the end of the Second World War when Schloss Waldhof, about 20 km from Königsberg, where museum specimens had been taken for safe-keeping, was shelled and completely destroyed by fire (pers. comm. Prof. Dr O. Koehler (1972), director of the Königsberg Museum until 1945).

The preserved material of *Equus quagga quagga*, including the above specimens, now consists of:

- skins—23, plus 1 mounted head and neck
- complete skeletons—7
- skulls—20, including 7 from complete skeletons; at least 3 of the mounted skins appear to contain skulls
- loose skeletal parts—2 sets of foot bones; upper and lower incisivae in portion of jaws
- other—dried connective tissue, flesh, etc., removed from skin; nasal cartilages and palate removed from skull (in alcohol) (Rau 1974: 58)

NOTES ON BURCHELL'S ZEBRA AND QUAGGA

During February to October 1977 approximately 400 privately owned skins of plains zebra *Equus quagga (burchelli)* and mountain zebra *Equus zebra hartmannae* were processed at a Cape Town tannery and examined by the author. These originated from many different localities in southern Africa. Skins of 113 plains zebras were photographed, the initial 88 non-selectively and



Fig. 4. Königsberg quagga (destroyed), adapted from Hilzheimer (1930).

the remaining 25 selectively. The proportion of the two species processed during a two-month period (February and March) was 88 plains zebra: 62 mountain zebra.

A great number of 'subspecies' and even 'species' of plains zebra have been described. In bestowing names to the many variations, the stripe pattern has been the principal, and often the only, character considered (Ansell 1971). This is certainly true in the case of the 'subspecies' *burchelli*.

The diagnostic characteristics of the true Burchell's zebra *Equus quagga burchelli* are usually given as follows: whitish, unstriped legs except occasionally some traces of stripes on the hocks (Pocock (1897: 52) accepts some stripes on the 'knees' as well); basic colour of dorsal parts white to ochre and brownish; interspaces with shadow-stripes, which may be broad and intense, or less conspicuous; body-stripes not meeting the ventral midline.

Equus quagga antiquorum is defined by the striping extending on to the legs to at least the 'knees' and hocks, but sometimes to the pasterns.

Equus quagga burchelli (*E. burchelli burchelli*) is one of the few still recognized as a valid subspecies. The accepted distributional range of this subspecies included the Orange Free State, the north-eastern Cape Province, southern Botswana and the south-western Transvaal. As zebras no longer occur in these regions, other than reintroduced specimens, the true Burchell's zebra is usually considered to have been extinct since about 1910.

The locality of the type specimen on which Gray (1825) based the description of the subspecies is between Campbell and the Vaal River. The specimen figured as *Equus quagga burchelli* by Antonius (1951, fig. 22) originated from British Bechuanaland (Botswana) and lived at Hagenbeck's Tierpark, Germany, during 1907-9. However, most preserved specimens of this subspecies lack locality data, as do those individuals that lived at menageries or zoos and are known from illustrations and/or descriptions.

It appears, therefore, that the accepted range is based on old reports rather than collected material, and that the true range is not known. Indeed, different opinions as to the range of *Equus quagga burchelli* have been expressed. Matschie (1894) has included Zululand while Shortridge (1934) and Eloff (1967) extend the range to Great Namaqualand (South West Africa). The concept of the range of a subspecies within the continuous distribution of a species is open to question, especially in the case of fast-moving and migrating animals such as the plains zebra. With regard to zebra distribution, Tegetmeier & Sutherland (1895) wrote: 'Disputing, therefore, as to whether two closely allied animals are specifically or sub-specifically distinct is almost a waste of words. We know that a species spread over a wide area will change according to the conditions of life, until at last the two extremes are so diverse as to be regarded as distinct species, but no one can say where one species ends and the other begins, for they merge gradually into each other.'

The uncertainty about the former range of the subspecies *Equus quagga burchelli* has been aggravated by the indiscriminate use of the names 'quagga'

and 'Burchell's zebra', and by the difficulty in distinguishing between those two forms as well as between the true Burchell's zebra and its northern relatives.

Accurate assessment of old documents is, therefore, practically impossible. Pocock (1897: 42) wrote 13 years before the alleged extinction of *Equus quagga burchelli*: '... and on account of the general application of the term *Burchelli* to any or all of its subspecies, we are in ignorance of the exact area that it now occupies in S. Africa.'

If all the mounted zebra specimens preserved in museums had precise locality data, there would be in all probability *antiquorum*-types from the *burchelli* 'range' and vice versa. Since most older mounted zebras do not, however, have conclusive locality data, it is accepted that apparent *burchelli* specimens originate from the accepted *burchelli* range while *antiquorum* patterned specimens are thought to be from further north. Since the plains zebra has a continuous distribution, recent interferences by man excepted, within which certain forms or variations predominate in certain areas, it follows that, in intergradational areas between two forms, the one form will gradually decrease in percentage of total numbers as the area of the next form is approached.

Despite the fact that for most of the preserved or known plains zebra specimens, which conform basically to the description of *Equus quagga burchelli*, the place of origin is not known, they are accepted as belonging to that subspecies, as is shown in the figures by Cabrera (1936) (Fig. 5) and Antonius (1951).

The subspecies *Equus quagga antiquorum* is presently considered to include all the extant southern forms of the plains zebra, ranging from southern Angola and (historical) Damaraland through Botswana and Transvaal to Zululand. Consequently, individual variation within *antiquorum* is considerable (Fig. 6). Eloff (1967) stated that the three subspecies *antiquorum*, *chapmani* and *wahlbergi* occur together in Zululand. Antonius (1951) had observed that in Damara zebra and especially in Wahlberg zebra *burchelli*-like individuals do occur.

However, such individuals originate from outside the presumed range of the true Burchell's zebra and are consequently not accepted as such. Nevertheless, some authors are cautious. Cabrera (1936: 94), while saying that the subspecies 'appears to be extinct', also states, 'in fact, I regard as typical *burchelli* all members of the species having all four legs white from the elbow and the stifle joint, except for the occasional presence of a few short markings across the hocks, and with the thighs free of complete and well-defined dark stripes behind the stifle stripe'. Dorst & Dandelot (1970) list the subspecies *burchelli* as 'probably extinct'.

Amongst the extremely variable skins (many with numerous small, light dots in stripes and shadow-stripes) examined at the tannery, were several specimens from a Zululand game farm with a surprising combination of light basic colour and few and/or weak shadow-stripes and considerable stripe reduction (Fig. 7A). It is generally believed that the change in coloration of plains zebras to the south of their distributional range is achieved by stripe-

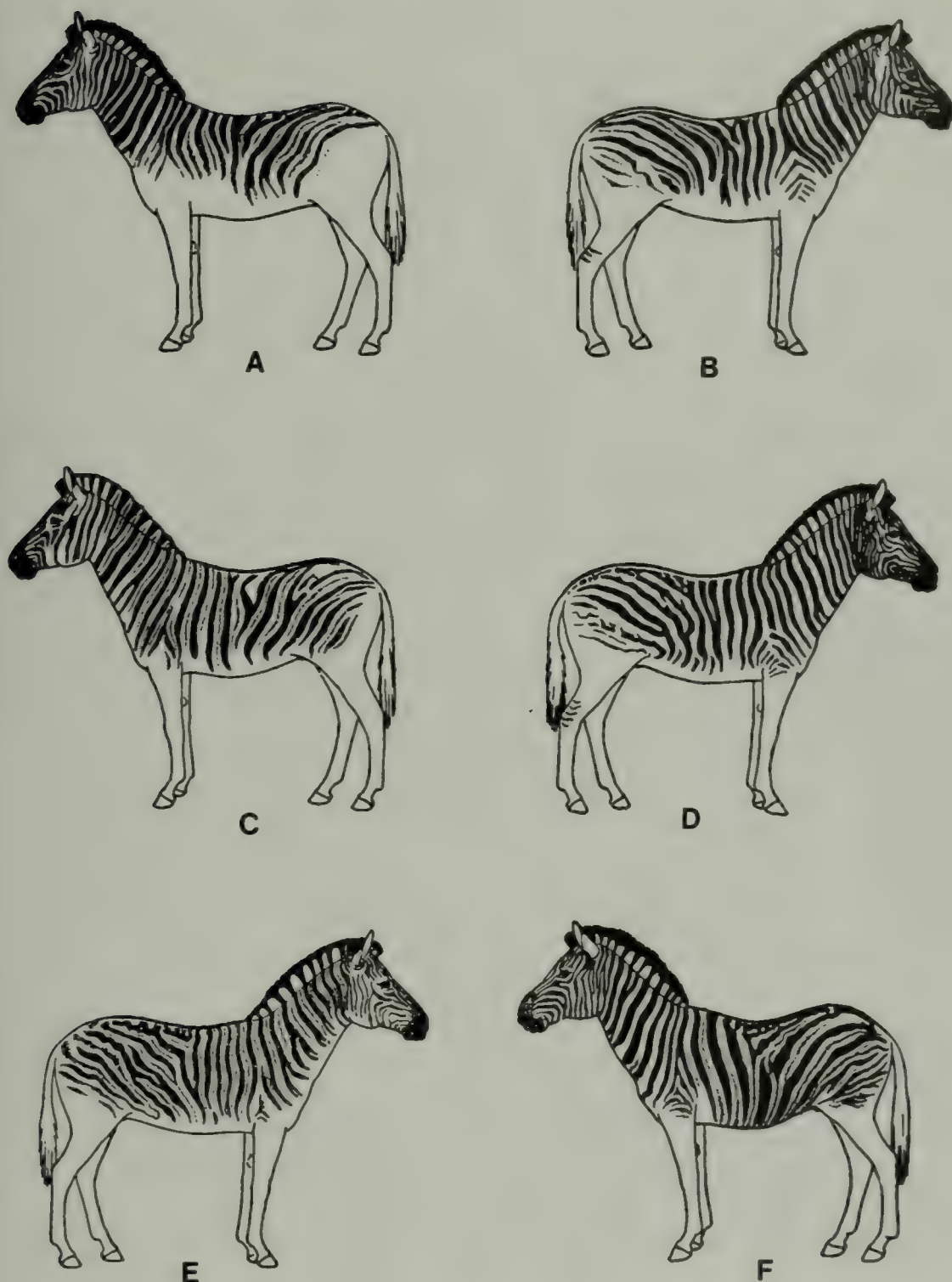


Fig. 5. Examples of true Burchell's zebra, *Equus quagga burchelli*, shown in standardized outline. A. Type of '*Equus burchelli paucistriatus*' Hilzheimer, 1912, at Mainz Museum. B. Animal that lived at Jardin des Plantes, Paris, 1826. C. Type of subspecies from Little Klibbolikhonnifontein, British Museum (Natural History) (destroyed). D-E. Animals that lived at Knowsly Park, about 1845. F. Animal that lived at Zoological Garden, Dresden. (Adapted from Cabrera (1936).)

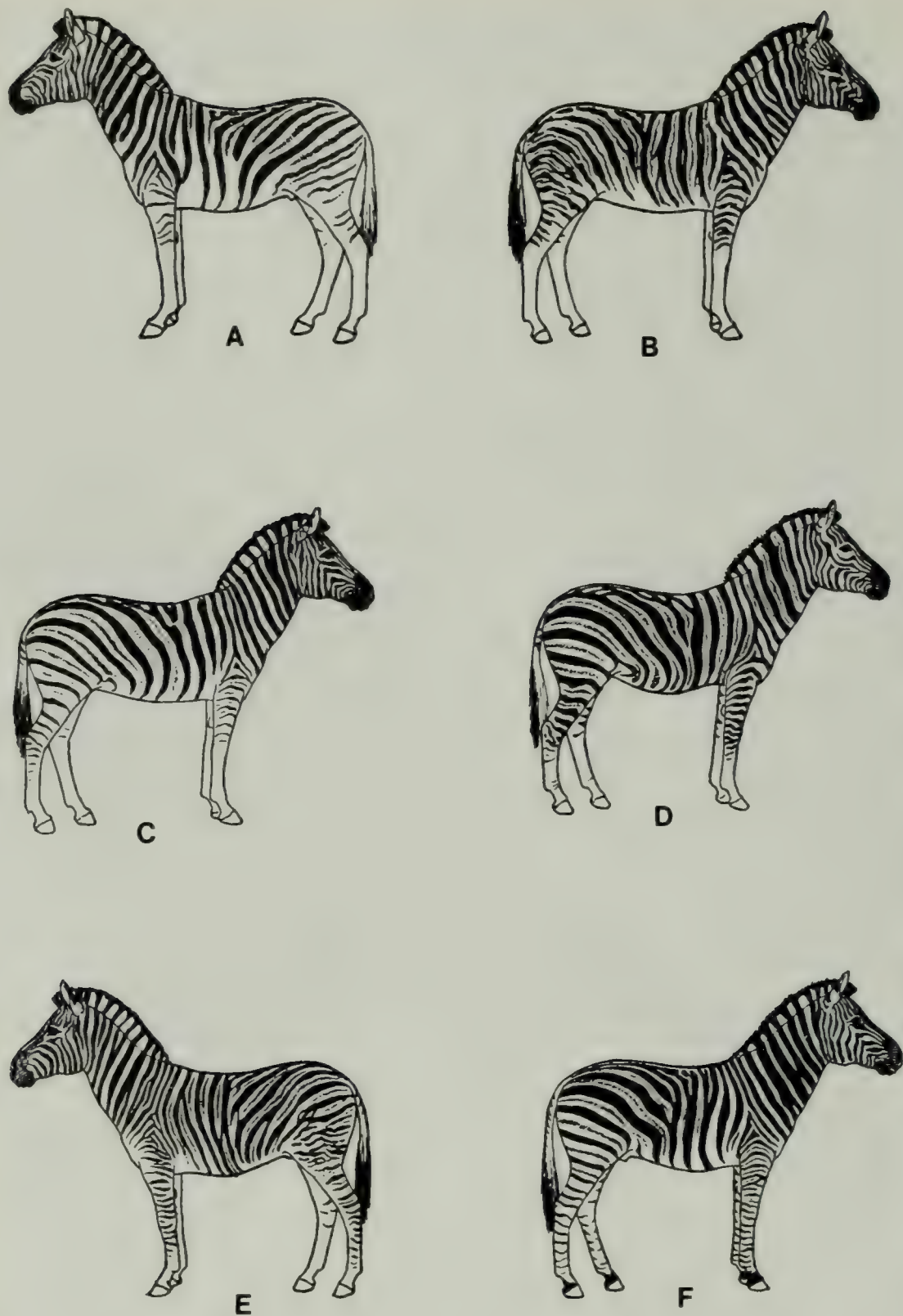


Fig. 6. Examples of *Equus quagga antiquorum*, shown in standardized outline. A. From Rietfontein West, Munich Museum. B. Type of subspecies from Angola (Smith 1841). C. From eastern Transvaal. D. From west of Lake Ngami. E. From Zululand. F. From eastern Transvaal. (Adapted from Cabrera (1936).)

reduction and the darkening of basic colour and the occurrence of shadow-stripes. However, the above specimens indicate that these processes do not necessarily occur together. Indeed, there are specimens from other areas which, in spite of more extensive striping, display dark basic colour (Fig. 8A), some with numerous strong shadow-stripes (sometimes three in one interspace). From the Zululand skins (Fig. 7) and additional photographs it appears that stripe-reduction is the dominant feature in this eastern population, while to the west on the interior plateau the darkening in both basic colour and through shadow-stripes is more pronounced.

In terms of stripe reduction these Zululand skins certainly do not fit into the concept of *Equus quagga antiquorum* (Fig. 6), but they do agree with the description of *Equus quagga burchelli*. Indeed, a few are less striped than some of the *burchelli* specimens figured by Cabrera (1936) (Fig. 5) and others. It appears, therefore, that *Equus quagga burchelli* is, in fact, not extinct but still survives in Zululand (and possibly Swaziland), and that its range does extend eastward into Zululand, as Matschie (1894) stated. (The 'myriads of Quaggas' which Chapman (1868, cited in Antonius 1951: 96) encountered in the extreme north-eastern Orange Free State could thus have been true *burchelli*, and not as Antonius (1951: 96) considered, Wahlberg zebra.) Otherwise the subspecies *burchelli* would have to be considered as part of the *antiquorum* complex, a thought similarly expressed by Rzasnicki (1951) and Roberts (1951), cited in Ansell (1971). The only other alternative would be not to recognize such individuals (Figs 7B–D, 9B, D) as members of the subspecies *burchelli*. However, had they been old mounted specimens, they would be regarded as true Burchell's zebras.

It must be noted that the farm where these specimens had been shot is a hunting farm which was originally stocked with 300 zebras from Hluhluwe Game Reserve, and that hunters select the most striped specimens (C. Tinley, pers. comm.). Selective breeding is thus exercised unintentionally and this might have 're-created' *burchelli*, although similar specimens do occur in Hluhluwe and Umfolozi Game Reserves, the only area in Zululand where the original zebra population has not been interfered with through reintroductions (P. M. Brooks, pers. comm.).

Zululand undoubtedly is an inter-gradational area between the two forms *burchelli* and *antiquorum*. Observations made during a recent visit to that area and Swaziland suggest that the percentage of *burchelli* types may be as high as 15 in Zululand, although P. M. Brooks, biologist at Hluhluwe, estimates it to be 5–10 per cent (pers. comm.).

The north-eastern and eastern parts of Swaziland also retain an endemic population of plains zebra (T. E. Reilly, pers. comm.). There is no geographic barrier between Zululand and the Swaziland lowveld, and it is not surprising that some of the zebras observed there fit or approach the description of *Equus quagga burchelli*, though the percentage of such specimens must be expected to be lower than further south.

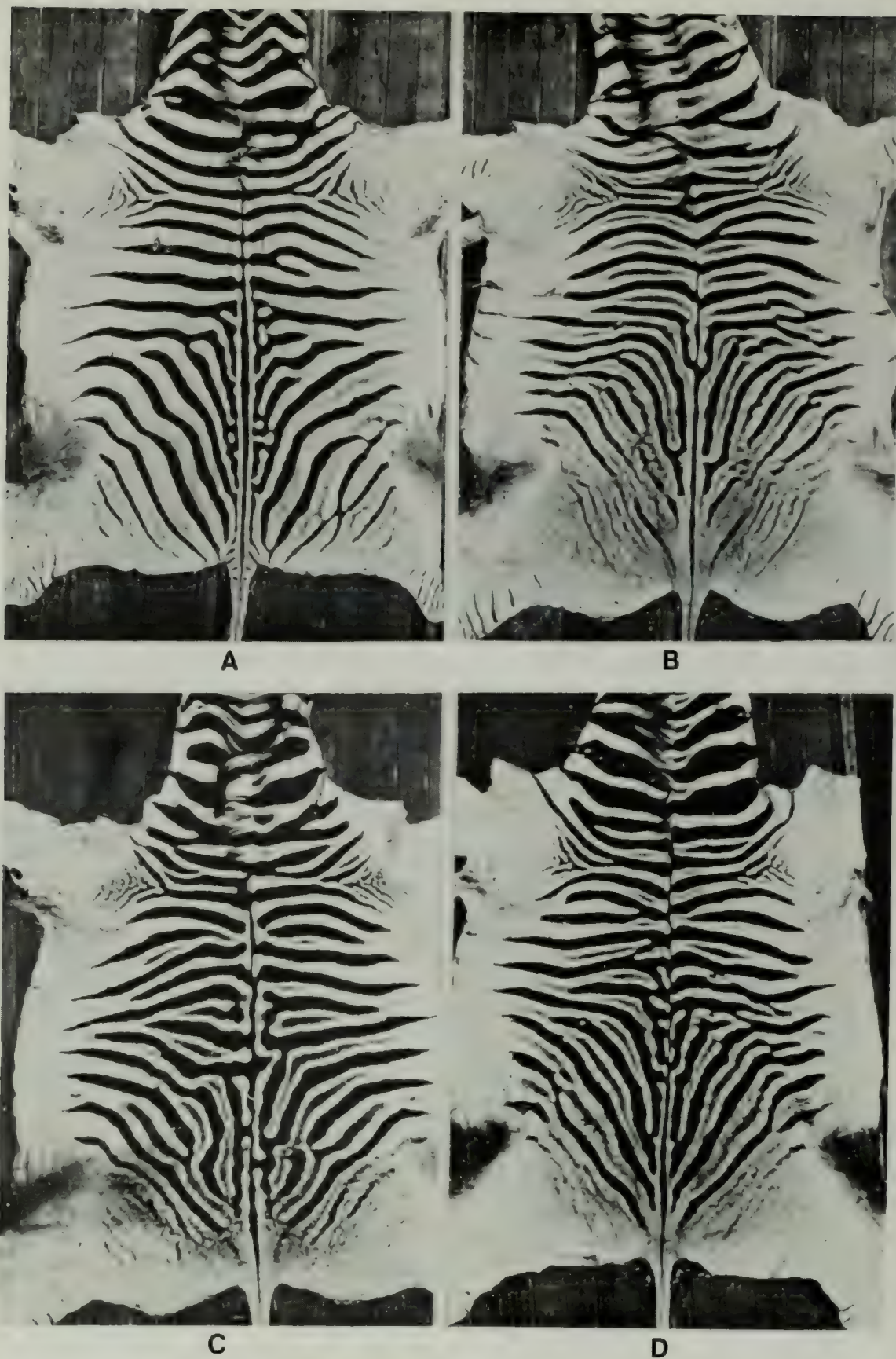


Fig. 7. Skins of plains zebras from Zululand, 1977. A. Note stripe-reduction, few shadow-stripes. B-D. Note shadow-stripes on neck and stripe-reduction. (B now at South African Museum, ZM38819.)



Fig. 8. Skins of plains zebras from southern Africa. A. Precise locality unknown; note dark basic colour of upper parts compared to lower leg. B. Precise locality unknown; note numerous shadow-stripes and extensive striping. C. From game farm in Zululand; note dark basic colour of upper parts. D. From southern Kaokoveld, South West Africa; note little contact between body-stripes and dorsal midline.

Despite the uncertainty whether the 'quaggas' of old reports were, indeed, the true quagga, *Equus quagga quagga*, the northern boundary of its range is usually considered to have been formed roughly by the Orange and Vaal rivers. The eastern limit might have been about the boundary between the Orange Free State and Natal (Grout, cited in Shortridge 1934: 402). It is also generally accepted that the ranges of quagga and true Burchell's zebra overlapped in the Orange Free State (Antonius 1951; Liebenberg 1964; Ansell 1971).

Antonius (1951) was of the opinion that the quagga, being essentially a form adapted to the Karoo and possibly the most distinct of all the plains zebra subspecies, expanded its range secondarily in a northerly direction and met and overlapped along a broad front with the southward expanding Burchell's zebra. He obviously did not believe in reports about the social and reproductive separation of the two forms, since he considered one of the preserved quagga specimens (the more striped specimen of '*Equus burchelli paucistriatus*' at Mainz (Fig. 9A and Rau 1974, fig. 13) as a possible cross between the two forms (Antonius 1951: 26).

It is difficult to accept that separate herds of the two forms existed in the same locality. Even if they did represent separate species, as some are inclined to believe, herds formed by members of both must be expected, since this is known to occur in extant zebra species where their ranges overlap. For example, *Equus zebra hartmannae* overlaps with *Equus quagga antiquorum* in South West Africa (Antonius 1951: 82) and *Equus grevyi* forms mixed herds with *Equus quagga boehmi* in Kenya (Antonius 1951: 82; Bartlett 1963). Even true quaggas were seen together with the Cape mountain zebra at Geelbeckfontein, at the southern limit of the Karoo, by Barrow (1801, cited in Antonius 1951: 82).

As shown previously (Rau 1974) the quagga and the true Burchell's zebra approach one another in basic colour and in stripe reduction, so much so that some of the preserved specimens (e.g. Rau 1974, fig. 12 right) have variously been regarded as one or other of the two. Furthermore, some of the characteristics previously considered to be typical of the quagga (Rau 1974) have been observed in the skins at the Cape Town tannery and in a specimen from Kruger National Park. These characteristics include narrow interspaces (Smuts 1974, fig. 1.4.5), dorsal midline being flanked by a light band on either side, and body-stripes not in contact with dorsal midline except sometimes via narrow bridges (Fig. 8D).

Antonius (1951: 29) has already pointed out that the quagga had reddish dark-brown stripes which, especially on the body, merge into the reddish basic colour. It has previously been explained why the coloration of the quagga has been incorrectly interpreted as light stripes on a dark background (Rau 1974: 43). Careful examination reveals beyond all doubt that the quagga, like all the other plains zebras, is dark-striped and that the interspaces darken progressively from the shoulder in a posterior direction until they become equal in tone with stripes and shadow-stripes to produce the 'uniform' posterior portion. In other southern plains zebras the interspaces are also lightest on head and neck. Ansell (1971: 5)

and others are wrong in defining the striping in the quagga as 'whitish on dark background'.

Since identification is therefore complex, and since it is impossible to observe the stripe pattern of each individual when looking at a herd, the alleged recognition of separate herds of quaggas and Burchell's zebras in the same locality must be treated with suspicion.

The grouping of plains zebras into subspecies is thus somewhat vague, or, as it is expressed by Ansell (1971) 'has never been satisfactory'. In an attempt to sort out this confusion, Pocock (1897) pointed out that throughout the distribution area of the plains zebra 'intermediate types' do exist between particular forms which prevail in particular localities. In addition, as mentioned earlier, typical representatives of the two forms occur in intergradational areas, the closer to the area of the one form the lower the percentage of the other form.

The high degree of variability, both between geographically distant populations and within one herd, has been attributed by Antonius (1951) to the process of eliminating the contrasting stripe-pattern. It should be noted that Antonius's 'Rückbildung der Bein- und Rumpfstreifung' has been misinterpreted by Eloff (1966, 1967) as being a sign of genetic pauperization.

As shown above, the gradual change from one form to another in plains zebras appears to include, at least in exterior characteristics, the 'separation' into *Equus quagga* and *Equus burchelli*. Relatively few skulls of the true quagga are available and some of these lack sufficient data to establish their authenticity. The fact that some skulls may have been obtained by breaking up an old stuffed quagga skin (as has happened at Berlin, where the skull was later identified as that of *Equus caballus* (Antonius 1951: 35)) is no guarantee of their identity as *Equus quagga quagga*.

However, some zoologists believe that there are specific morphological differences between skulls of the quagga and the plains (Burchell's) zebra (e.g. Cooke 1950; Lundholm 1951; Gentry 1975; V. Eisenmann, pers. comm.). The recent study by V. Eisenmann (pers. comm.) has shown that in some skull characters there is a cline from northern to southern plains zebras. In other words, in some respects at least skulls of southern plains zebras approach those of the quagga more closely than do northern forms. This conforms to the well-documented cline in colour and stripe-pattern.

To conclude, it would appear that the Burchell's zebras and the quagga should be regarded as one species, *Equus quagga*. Furthermore, since the grouping into subspecies, either by appearance or by distribution, is not clear-cut in the case of the plains zebras, it might be preferable to refer them to forms, types or variations prevailing in certain areas, rather than to subspecies.

REINTRODUCTIONS OF ZEBRAS

The reintroduction of animal species into areas where natural populations have been exterminated is increasingly common. There are, however, problems with this practice, some of which have been discussed by Greig (1977).

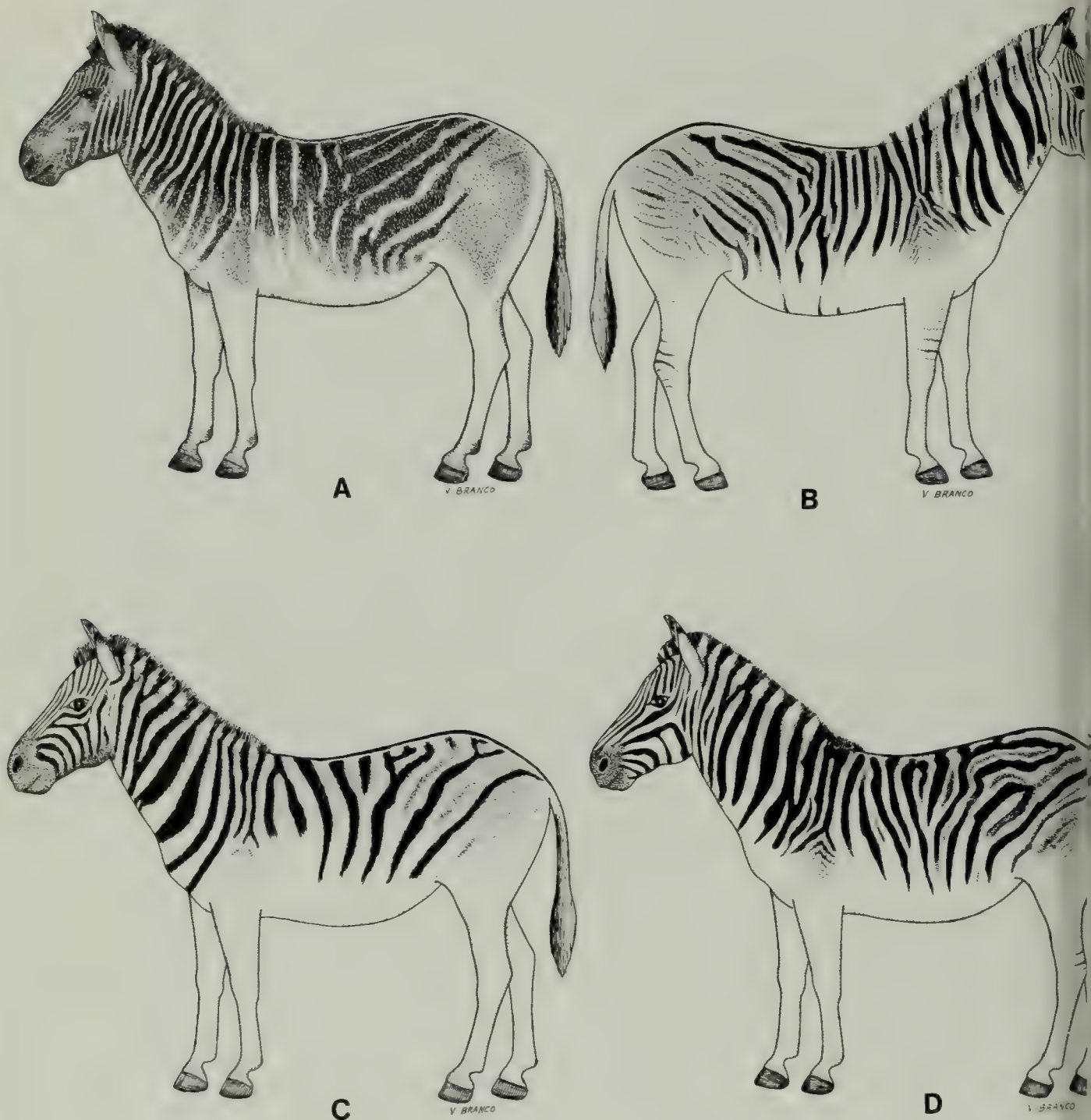


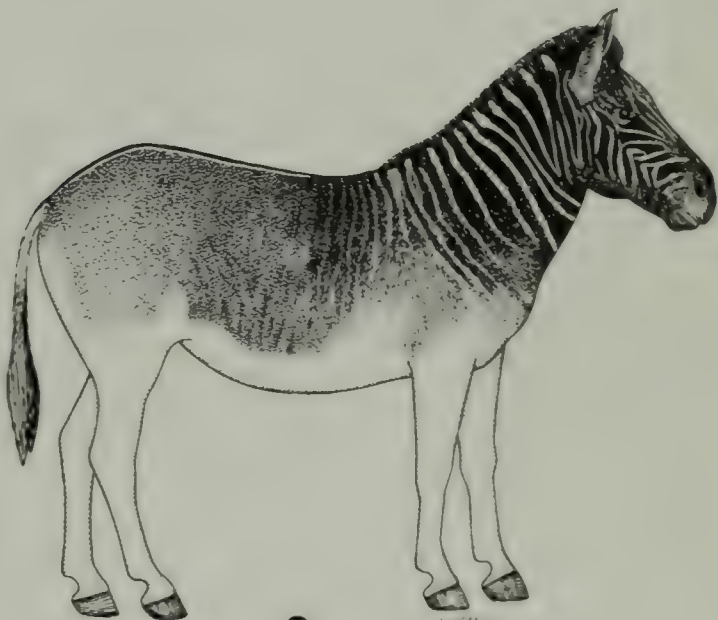
Fig. 9. Stripe patterns and tone of basic colours of various plains zebras, shown in standardized outline. A. Female quagga at Mainz Museum. B. Burchell's zebra from Zululand (same as Fig. 7B). C. Male Burchell's zebra at Leiden Museum. D. Burchell's zebra from Zululand (same as Fig. 7D). E. Quagga at Tring Museum (near London). F. Type of true Burchell's zebra, British Museum (Natural History) (destroyed). G. Quagga at Berlin Museum. H. Male quagga at Mainz Museum. I. Burchell's zebra at Mainz Museum (type of '*Equus burchelli paucistriatus*' Hilzheimer, 1912).



E



F



G



H



I

Both plains and mountain zebras are amongst those South African mammals whose ranges have been much restricted during the past three centuries. Now, and in the recent past, zebras are being translocated from areas where populations survive to areas which they formerly inhabited. In the case of the plains zebras such reintroductions have involved the movement into certain areas of forms dissimilar to those which previously occurred there, even though the original form, or one close to it, still exists.

As indicated above, the 'subspecies', *Equus quagga burchelli*, apparently survives in Zululand and thus, when reintroductions of zebras into the former range of the true Burchell's zebra are contemplated, it would be desirable that selected specimens from Zululand be used, rather than animals of the *antiquorum* type. It would even be desirable to eliminate former indiscriminate reintroductions and to replace them with individuals which are closer to the original population. With a minimum of initial selective breeding in order to eradicate recessive *antiquorum* characteristics, which are present also in *burchelli*-like individuals from Zululand (an intergradational area between the two forms), a 'pure' population of plains zebras resembling the former endemics could be achieved within a relatively short period.

ACKNOWLEDGEMENTS

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6. **SYSTEMATIC** papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierti Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

- The Figures, Maps and Tables of the paper when referred to in the text
e.g. '... the Figure depicting *C. namacolus* ...'; '... in *C. namacolus* (Fig. 10) ...'
- The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene
- Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as

'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

R. E. RAU

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MATERIAL OF THE EXTINCT CAPE COLONY
QUAGGA AND NOTES ON THE RELATIONSHIP AND
DISTRIBUTION OF SOUTHERN PLAINS ZEBRAS

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ANNALS

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Number of illustrations (figures, enumerated maps and tables, in this order)
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- (c) *Table of contents* giving hierarchy of headings and subheadings
- (d) *Introduction*
- (e) *Subject-matter* of the paper, divided into sections to correspond with those given in table of contents
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3. MANUSCRIPT, to be submitted in triplicate, should be typewritten and neat, double spaced with 2,5 cm margins all round. First lines of paragraphs should be indented. Tables and a list of legends for illustrations should be typed separately, their positions indicated in the text. All pages should be numbered consecutively.

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Footnotes should be avoided unless they are short and essential.

Only generic and specific names should be underlined to indicate italics; all other marking up should be left to editor and publisher.

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'Smith (1969) describes ...'

'Smith (1969: 36, fig. 16) describes ...'

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'As described (Haughton & Broom 1927) ...'

'As described (Haughton *et al.* 1927) ...'

Note: no comma separating name and year

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names of joint authors connected by ampersand

et al. in text for more than two joint authors, but names of all authors given in list of references.

(b) Full references at the end of the paper, arranged alphabetically by names, chronologically within each name, with suffixes *a*, *b*, etc. to the year for more than one paper by the same author in that year, e.g. Smith (1969a, 1969b) and not Smith (1969, 1969a).

For books give title in italics, edition, volume number, place of publication, publisher.

For journal article give title of article, title of journal in italics (abbreviated according to the *World list of scientific periodicals*, 4th ed. London: Butterworths, 1963), series in parentheses, volume number, part number (only if independently paged) in parentheses, pagination (first and last pages of article).

Examples (note capitalization and punctuation)

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FISCHER, P.-H. 1948. Données sur la résistance et de la vitalité des mollusques. *J. Conch.*, Paris 88: 100-140.

FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* 74: 627-634.

KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) 2: 309-320.

KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* 17 (4): 1-51.

THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* 4: 269-270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* 16: 269-270.

(continued inside back cover)

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REDESCRIPTION OF *PLIOPLATEIA* K. H. BARNARD,
A GENUS OF AMPHIPOD (CRUSTACEA) FROM
SOUTH AFRICA

By

J. LAURENS BARNARD

Cape Town Kaapstad

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A GENUS OF AMPHIPOD (CRUSTACEA) FROM SOUTH AFRICA

By

J. LAURENS BARNARD

Department of Invertebrate Zoology, Smithsonian Institution, Washington

(With 4 figures)

[MS. accepted 12 September 1978]

ABSTRACT

Plioplateia K. H. Barnard (1916) is removed from Phliantidae to form the type genus of a new family demonstrating evolutionary outflow from the southern Pacific family Ceinidae towards the circumtropical family Phliantidae. At least nine major characters constrain *Plioplateia* from assignment to Phliantidae. *Plioplateia* appears to be the last living relict of what may have been a diverse group of taxa standing between ceinids and phliantids. It joins many other South African amphipods now considered to be relicts.

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INTRODUCTION

Plioplateia, a gammaridean amphipod, was described by K. H. Barnard (1916) and placed in the family Phliantidae. Since that time many genera in this evolutionary vicinity have been described and then later realigned, mainly by J. L. Barnard (1972*a*, 1972*b*) and Griffiths (1975), into families Phliantidae, Temnophliidae, Kuriidae and Ceinidae, with subfamily Chiltoniinae. *Plioplateia* appears to stand between Ceinidae and Phliantidae but differs in so many ways from either family group that a new family is established for *Plioplateia*. All of these families are included in the superfamily Talitroidea.

The Plioplateidae join the Temnophliidae of South Africa as the narrowest relict families known in the Gammaridea except for the Kuriidae from Abd-el-Kuri near the Gulf of Aden. South Africa is noted for other isolated or relict amphipods, mainly the genera *Calliopiella* Schellenberg, *Cypsiphimedia* K. H. Barnard, *Dikwa* Griffiths, *Triodos* K. H. Barnard, *Hoplopleon* K. H. Barnard, *Exampithoe* K. H. Barnard, *Macropisthopus* K. H. Barnard, *Unciolella* Chevreux, *Elasmopoides* Stebbing, *Cunicus* Griffiths and *Phoxostoma* K. H. Barnard.

Plioplateidae fam. nov.*Type genus*

Plioplateia K. H. Barnard, 1916.

Diagnosis

Talitroidea with laterally compressed tall, cuspidate bodies but coxae poorly splayed and excavate or cuspidate; coxa 4 small. Cuticle humped and rough. Head dorsoventrally compressed, complexly cuspidate. Antennae disparate, cuspidate, flagella elongate. Anterior part of body dorsally cuspidate. Mandibular molar huge, granular, not distinctly triturative. Inner lobes of lower lip well developed. Outer plate of maxilla 1 with eight spines. Inner plate of maxilla 2 much narrower and shorter than outer. Outer plate of maxilliped not larger than inner plate, palp articles 1 and 4 elongate, palp thin.

Gnathopods subchelate, hands expanded, lacking giant facial setae. Article 2 of pereopods 5–7 narrow, small.

Pleon small, deeply flexed below thorax, urosomite 3 distinct but vestigial. Pleopods elongate, peduncles thin, rami elongate, thin, uni-articulate. Uropod 3 formed of leaf-like peduncle lacking ramus. Telson forming erect cowl, deeply cleft.

Relationship

On first sight *Plioplateia* appears to belong to the Phliantidae as originally placed by K. H. Barnard, but *Plioplateia* differs from phliantids in the elongate flagella of the antennae, the elongate, thin pleopods with equal and uniarticulate rami, the giant mandibular molar, the presence of well-developed inner lobes on the lower lip, the small inner plate of maxilla 2, the small outer plate of the maxilliped, the thin maxillipedal palp with elongate article 1, the subchelate gnathopods lacking giant setae, and the cowl-like cleft telson. *Plioplateia* bears the bidentate pereonite 1 similar to that of many phliantids but would appear to be much more primitive and to share many features of the plesiomorphic Ceinidae (see J. L. Barnard, 1972a, 1972b). To a great extent *Plioplateia* fits many aspects of a model ancestor to phliantids with evolutionary outflow from ceinids, and, in addition, its isolation in South Africa fits the role of a relict.

Plioplateia shares the tall body and subchelate gnathopods of ceinids, and in many other characters (to follow) appears to have a foundation in *Taihape* J. L. Barnard (1972a) or *Waitomo* J. L. Barnard (1972a): size and flagellar condition of antennae in *Waitomo*; posterior dorsal cuspidation of *Waitomo*; molar of *Waitomo*; outer plate of maxilla 1 in both genera; maxillipedal palp of *Taihape*; gnathopods (less giant setae) and telson of either genus.

Plioplateia differs from Ceinidae in the dorsoventrally depressed head with complex cuspidation, the anterodorsal body cuspidation, the cuspidation and excavation of coxae and antennae, the special form of maxilla 2, the lack of

large setae on the gnathopods and the presence of inner lobes on the lower lip, wholly unique to *Plioplateia* in the Ceinid–Phliantid scheme.

The reduction in segmentation on the pleopods suggests that *Plioplateia* has progressed far from a perfect intergrade between ceinids and phliantids and this is also supported by the extra cuspidation on the head and coxae, the development of inner lobes on the lower lip, the reduction in size of the inner lobe on maxilla 1 and the outer plate of the maxilliped, the enlargement of the molar, the loss of giant setae on the gnathopods. The brood plates appear to be much larger than in ceinids and phliantids whereas the gills are much smaller. The weakly developed multispination on the apices of uropods 1–2 would appear to be a remnant of ancestry in ceinids where these spines are well developed.

The Kuriidae, composed only of *Kuria* Walker & Scott (1903), from Abd-el-Kuri, appear also to be in a level of evolution similar to *Plioplateia*. For example, the gnathopods of *Kuria* are subchelate, though weakly, the palms being almost transverse, and the outer plate of the maxilliped is small as in *Plioplateia*. Plioplateidae differ from Kuriidae in the ornamentation of the head, body and coxae, the small coxa 4, small article 2 of pereopods 5–7, expanded hands of the gnathopods, the disparity in sizes of antennae, and the extremely large mandibular molar. In minor ways, Plioplateidae differ from Kuriidae in the larger dactyls of the maxillipeds, and the absence of a ramus on uropod 3. Pleopods, maxillae and lower lip have not been reported for *Kuria*.

Plioplateia K. H. Barnard

Plioplateia K. H. Barnard, 1916: 155.

Type species

Plioplateia triquetra K. H. Barnard, 1916 (monotypy).

Diagnosis

With the characters of the family.

Description

Rostrum well developed, erect, thorn-like, bearing bilateral subsidiary tooth. Antenna 1 much longer than antenna 2, flagella of both pairs highly articulate, those of antenna 1 bearing 1–2 aesthetascs each. Epistome rounded anteriorly, upper lip deeply incised, asymmetrical. Mandibular incisor well toothed, right lacinia mobilis, if present, composed of three fused spines (or these actually rakers and lacinia mobilis absent), left lacinia mobilis large and well toothed, left mandible with three raker spines; molar very large, broad, blunt, tumid, poorly triturative, mainly granular apically; palp absent or possibly represented by small leaf. Lower lip with well-developed inner lobes. Outer plate of maxilla 1 with eight spines, palp uniarticulate, of medium size, bearing one medium apical seta. Inner plate of maxilla 2 much shorter and

narrower than outer, inner subconical, outer subrectangular, both poorly setose but inner with one medial and outer with two lateral setae. Inner plate of maxillipeds leaf-like, with tapered base, poorly armed, outer plates as large as inner; palp thin, article 1 elongate, article 4 unguiform, greatly elongate, with three apical setae. Pleurae of pereonites produced, rugose, humped or cuspidate.

Plioplateia triquetra K. H. Barnard

Figs 1-4

Plioplateia triquetra K. H. Barnard, 1916: 156, pl. 26 (figs 18-24); Griffiths, 1974: 328.

Diagnosis

With the characters of the family and genus.

Description

Head depressed but with erect thorn-like, rostrum with smaller basal tooth on each side, lateral lobes with weak dorsal and strong ventral tooth, middle of lobe bulging laterally and containing small but multifaceted ommatidial eye, antenna 1 inserted by sleeve into pocket anterior to ocular lobe, anteroventral area of head extended forward through fusion of articles 1 and 2 of antenna 2, lateral surface of article 2 with large cusp, article 3 also with large lateral cusp, gland cones emerging ventrally from fused article 2. Mouthpart field from lateral view, apart from maxillipeds, dominated by outer surface of lower lip.

Antenna 1 elongate, articles 1 and 2 cuspidate, article 3 shorter than article 1 of flagellum, latter 12-articulate, each article of flagellum with 1-2 aesthetascs and several curled setae. Accessory flagellum absent but marked by weak sinuate stripes inside of article 3. Antenna 2 small and slender, article 4 weakly cuspidate, article 5 slightly longer than article 4 of peduncle on article 1 of flagellum, latter 9-articulate, with short stiff curled setae.

Upper lip scarcely distinct from epistome, together rounded anteriorly, upper lip deeply bilobed. Each mandibular molar with large setule, right incisor with 8-9 teeth, left with 3, left lacinia mobilis with 7 teeth, right either absent or formed of 3 fused spines, left mandible with 3 distinct rakers each independent and mostly fused to mandible. Mandibular lobes of lower lip well developed, inner lobes distinct, thin across faces, broad, widely separating outer lobes. Inner plate of maxilla 1 linguiform, of medium size.

Wrist of gnathopod 1 longer than hand, shorter on gnathopod 2, neither lobate, palm well developed, oblique, defined by pair of spines, armed with pairs of wire-setules.

Coxa 1 apically expanded, with deep posteroventral notch, coxae 2-4 somewhat tapered, each with weak or moderate notch, coxa 4 smaller than coxa 1, not excavate posteriorly; coxae 5-7 short, coxae 5 and 7 bilobed and acuminate, coxa 6 trilobed and acuminate.

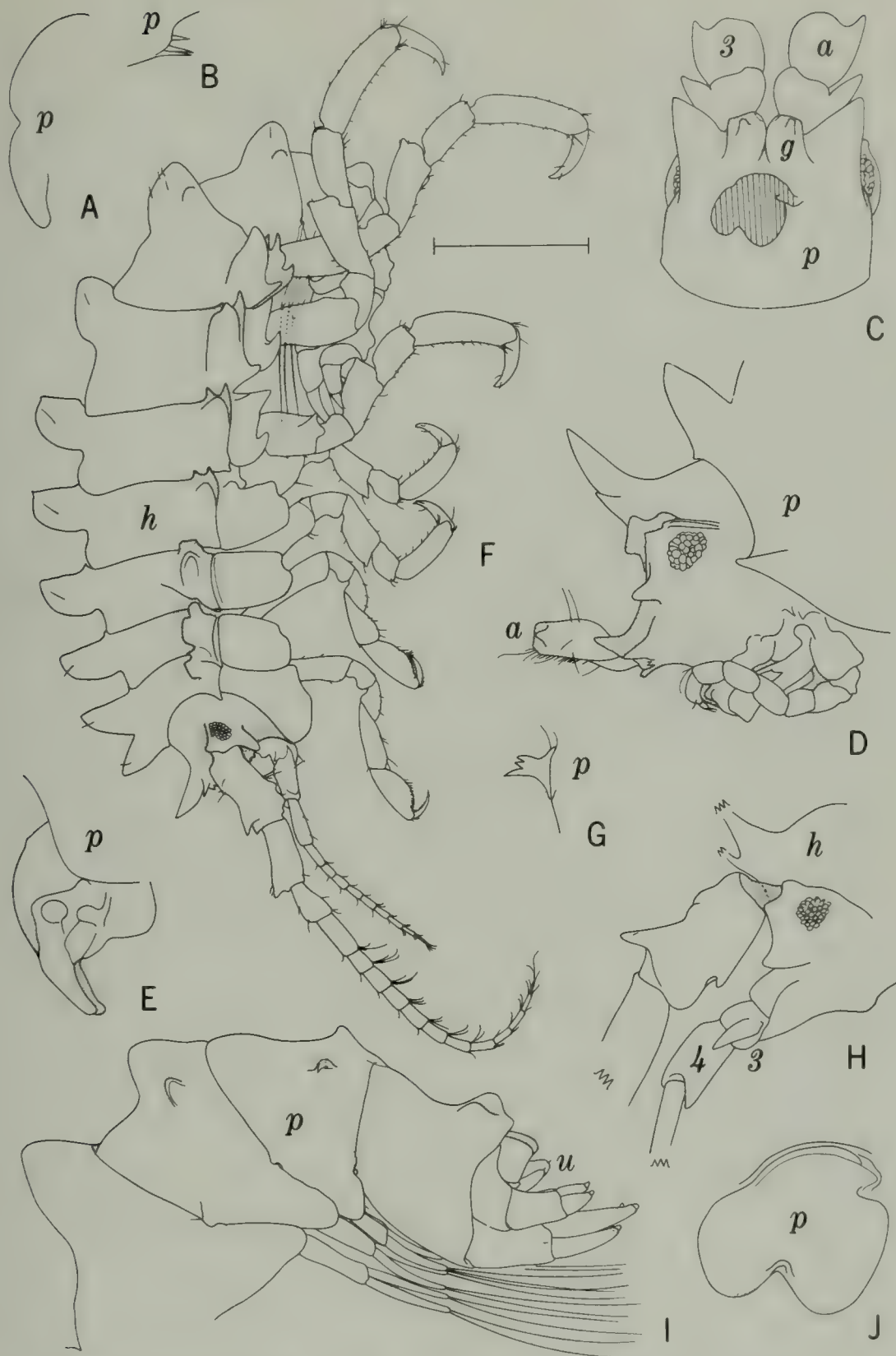


Fig. 1. *Plioplateia triquetra* K. H. Barnard. h, holotype, female 'h' unmeasured; p, male 'p' 5.72 mm. A. Prebuccal outline, left lateral. B. left mandibular rakers. C. Ventral view of head, upper lip hatched; a, antenna 2, g, gland cone. D. Head, lateral; a, antenna 2 broken off. E. Prebuccal, left lateral. F. Body, scale = 1 mm. G. Right mandibular rakers. H. Head. I. Pleon, left lateral; u, uropod 3. J. Upper lip, anterior.

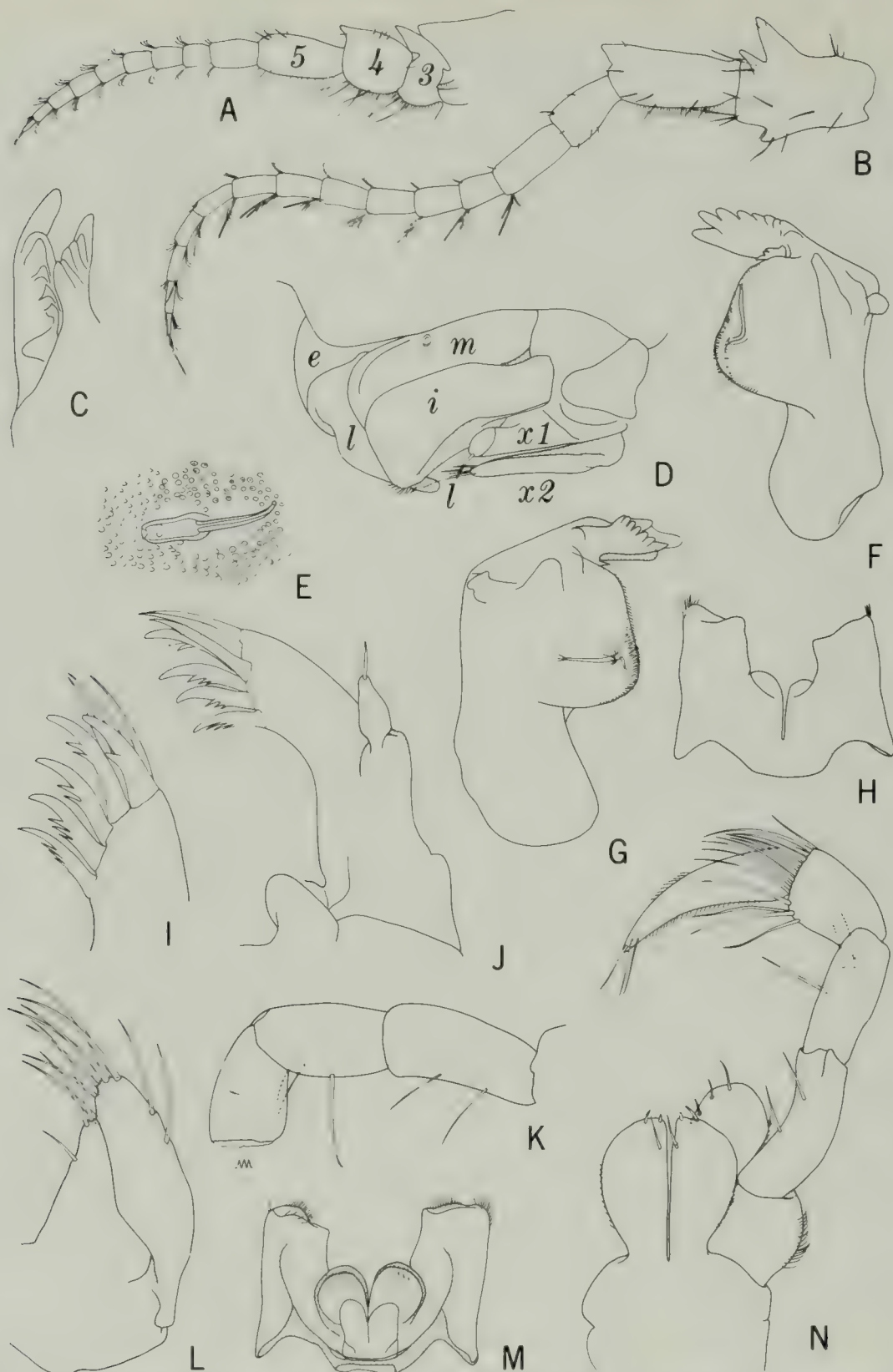


Fig. 2. *Plioplateia triquetra* K. H. Barnard. male 'p' 5,72 mm. A. Antenna 2. B. Antenna 1. C. Left mandible. D. Mouthparts, left side; e, epistome, i, lower lip, l, upper lip, m, mandible, x, maxilla. E. cuticle. F. Right mandible. G. Left mandible. H. Lower lip, oral side. I. Outer plate of maxilla 1. J. Maxilla 1. K. Palp of maxilliped, flattened. L. Maxilla 2. M. Lower lip, aboral side. N. Maxilliped.

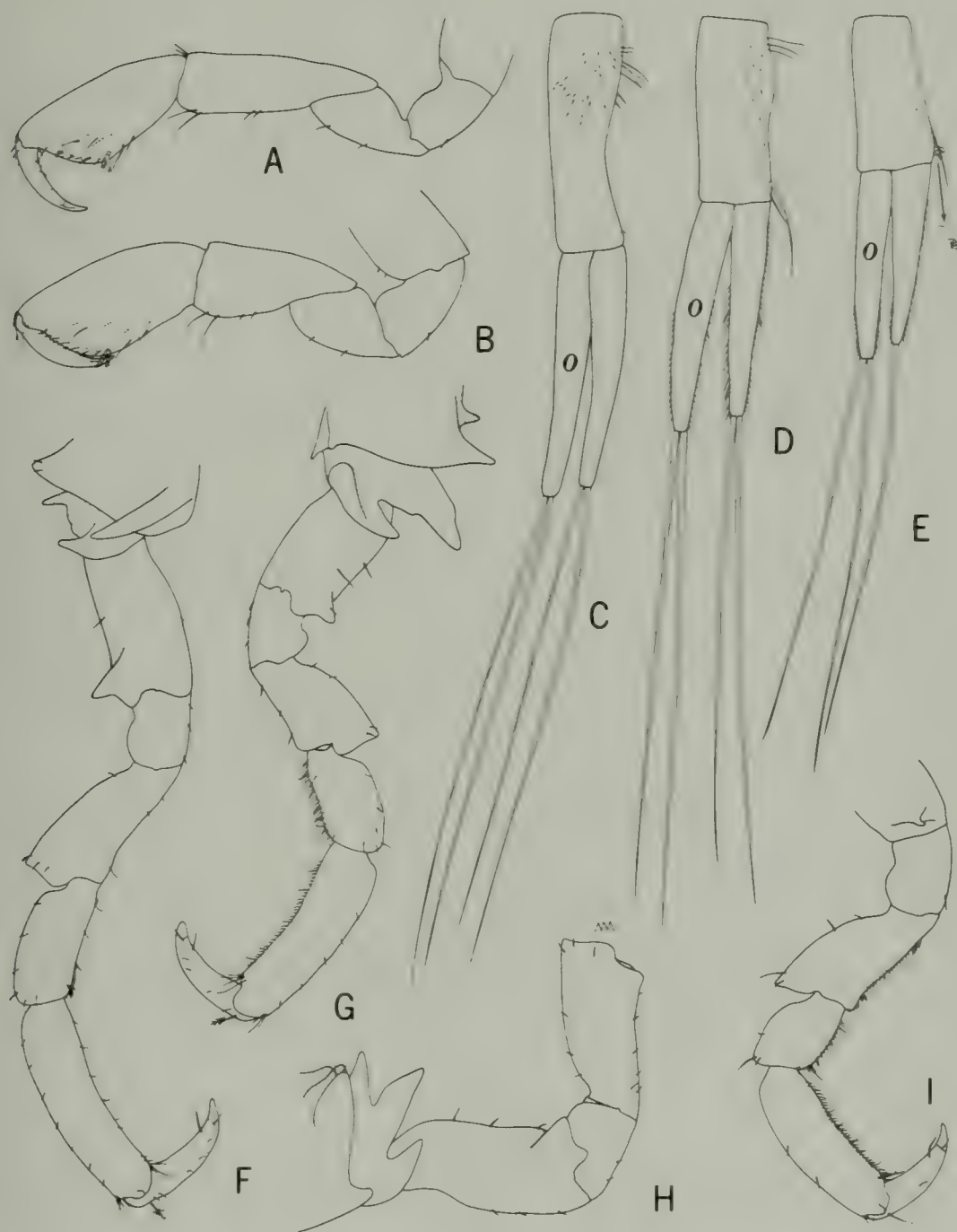


Fig. 3. *Plioplateia triquetra* K. H. Barnard. male 'p' 5.72 mm, o, outer ramus. A. Gnathopod 1. B. Gnathopod 2. C. Pleopod 1, rear. D. Pleopod 2, rear. E. Pleopod 3, rear. F. Pereopod 7. G. Pereopod 5. H. Pereopod 6. I. Pereopod 4.

Article 2 of pereopods 3-4 uncuspidate, that of pereopods 5-7 with bicuspidate posteroventral process; defining armaments on article 6 composed of setae. Coxal gills very small, attached to segments 2-6, somewhat triquetral (see appendages attached to figures of coxae 2-4). Brood plates very large, lamellar, attached to coxae 2-5, densely furnished with coil-tipped setae. Male penes of pereonite 7 highly lateral, just basal to coxae, very elongate and sausage-shaped.

Epimera tapering distally, poorly armed and unornamented. Pleopods tightly clumped, decreasing in size from front to rear slightly, inner rami scarcely shortened, each with 2 apical setae longer than ramus, except inner ramus of pleopod 3 with only one apical seta, peduncles elongate, only pleopod 3 with pair of apicomedial coupling spines.

Urosomite 3 vestigial, represented only by ventral plate, telson on dorsal side appearing attached directly to urosomite 2, telson formed of bifid cowl lacking macroscopic armament. Uropods 1-2 short, stout, poorly armed, outer

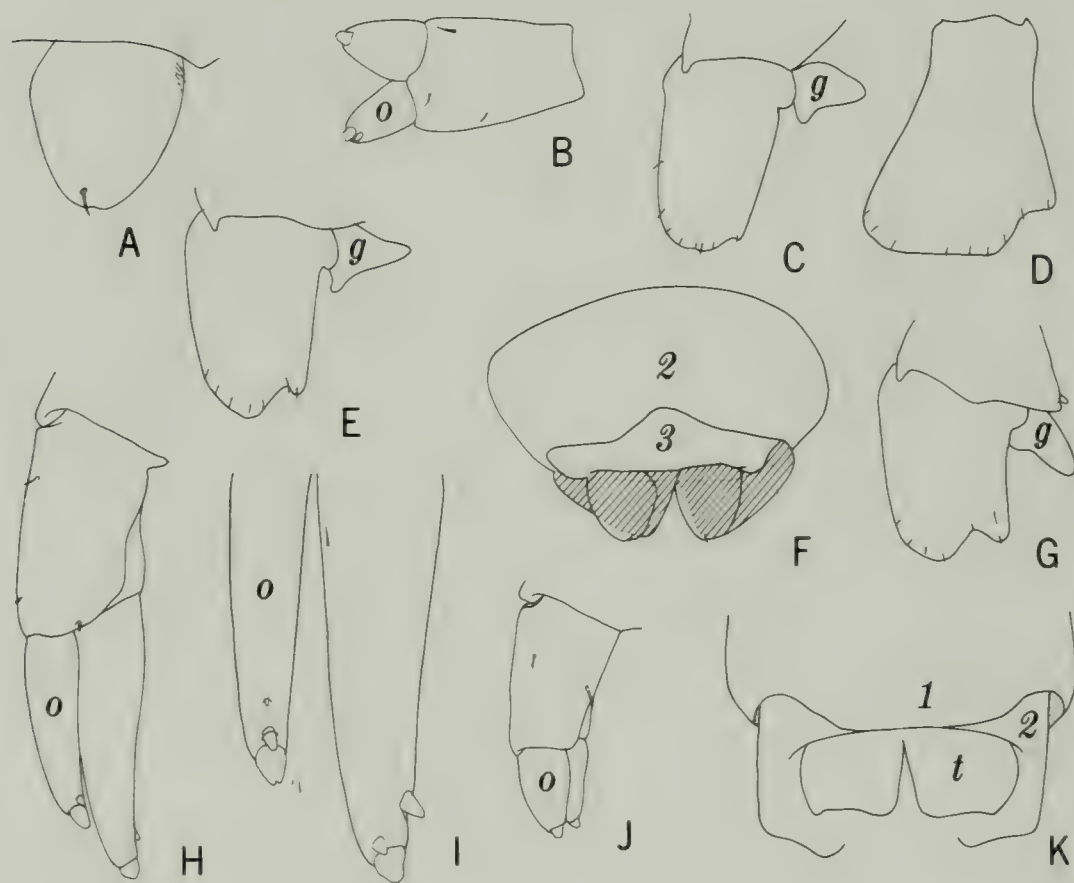


Fig. 4. *Plioplateia triquetra* K. H. Barnard. male 'p' 5.72 mm, g, gill, o, outer ramus. A. Uropod 3. B. Uropod 2. C. Coxa 2. D. Coxa 1. E. Coxa 3. F. Pleonite 6, ventral, telson hatched. G. Coxa 4. H. Uropod 1. I. Uropod 1, rami enlarged. J. Uropod 2. K. Pleonites 1-2 dorsal showing telson, t.

ramus of uropod 1 shortened, each ramus of both uropods with apical jewel-nail plus accessory spine except on inner ramus of uropod 2, inner ramus of uropod 1 with third spine fixed subapically. Uropod 3 ovate, bearing weak apical spinule.

Cuticle densely pebbled, each pebble usually complex, either with apparent pit or appearing ring-shaped (with central vacuole) bulbar setules sparse, pipes often abundant; no pits typical of ceinids have been observed.

Pereonite 1 with large tooth dorsally, remaining pereonites each with single tooth or hump, pleonites 1–3 each with increasingly smaller dorsal hump, urosomite 1 with slightly larger hump, this segment covering urosomites 2–3 dorsally; pereonites 1–7 from front to rear with increasingly complex distolateral rugosities or cusps.

Holotype

South African Museum A174, female 'h' (not measured to prevent damage) lacking right antennae, uropods 2–3, telson, right uropod 1.

Other material

South African Museum, University of Cape Town SCD 310 F, male 'p' 5.72 mm (dissected and illustrated herein).

Distribution

South Africa, 50–91 m.

ACKNOWLEDGEMENTS

I thank Dr C. L. Griffiths of the C.S.I.R. Oceanographic Research Unit, University of Cape Town, for locating this material, and Dr T. H. Barry Director of the South African Museum, for his kind assistance. Carolyn L. Cox of Smithsonian Institution inked and prepared the illustrations for publication; she also created several of the original drawings.

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An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierti Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

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Holotype

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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Capital initial letters

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e.g. '... the Figure depicting *C. namacolus* ...'; '... in *C. namacolus* (Fig. 10) ...'

(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names

e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene

(c) Scientific names, but not their vernacular derivatives

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Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as

'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

J. LAURENS BARNARD

REDESCRIPTION OF *PLIOPLATEIA*
K. H. BARNARD, A GENUS OF AMPHIPOD
(CRUSTACEA) FROM SOUTH AFRICA

S. Af. Capetown

VOLUME 77 PART 4

DECEMBER 1978

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- (f) *Summary*, if paper is lengthy
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FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* 74: 627-634.

KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) 2: 309-320.

KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* 17 (4): 1-51.

THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* 4: 269-270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* 16: 269-270.

(continued inside back cover)

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CRETACEOUS FAUNAS FROM ZULULAND AND
NATAL, SOUTH AFRICA
A NEW GENUS AND SPECIES OF GASTROPLITINAE
FROM THE MZINENE FORMATION (ALBIAN)

By

WILLIAM JAMES KENNEDY
&
HERBERT CHRISTIAN KLINGER

Cape Town Kaapstad

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By

WILLIAM JAMES KENNEDY

Geological Collections, University Museum, Oxford

&

HERBERT CHRISTIAN KLINGER

South African Museum, Cape Town

(With 7 figures)

[MS. accepted 20 September 1978]

ABSTRACT

Alopecoceras gen. nov., type species *Alopecoceras ankeritterae* sp. nov., is a unique Southern hemisphere homoeomorph of the Boreal genus *Neogastrolites* McLearn, 1930, which occurs in the low Middle Albian Mzinene Formation (Albian III) of the Mzinene River, Zululand. Whereas *Neogastrolites* evolved from *Gastrolites* McLearn, 1930, by acquisition of umbilical and ventral nodes and is of late Albian age, *Alopecoceras* is believed to be derived from *Hatchericeras* Stanton, 1910, by a similar acquisition of nodes. The genus also shows similarities to *Tetrahoplitoides* Casey, 1954.

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INTRODUCTION

The Mzinene Formation exposed along the Mzinene River 1 200 m north-east of the farm Amatis, north of Hluhluwe, Zululand (locality 35 of Kennedy & Klinger (1975: 28), 27°58'03"S, 32°18'34"E) has yielded a series of remarkable specimens which closely resemble the exclusively boreal late Albian ammonite genus *Neogastrolites* McLearn, 1930 (see Reeside & Cobban 1960 for extensive illustration of the genus) in association with a fauna of low Middle Albian age in part described by the authors in previous publications (Kennedy & Klinger 1977, 1978, in press; Klinger 1976; Klinger, Wiedmann & Kennedy 1975), and including *Carinophylloceras collignoni* Klinger, Wiedmann & Kennedy, *Ammonoceratites* (*Ammonoceratites*) *mahadeva* (Stoliczka), *Anagaudryceras buddha*

Ann. S. Afr. Mus. 77 (4), 1978: 57–69, 7 figs.

(Forbes), *Protanisoceras* (*Rossalites*) aff. *superbus* Collignon, *Lyelliceras* and *Douvilleiceras* species.

Further study has shown that the material represents a new genus and species which is a heterochronous homoeomorph of *Neogastrolites*, and is described below as *Alopecoceras ankeritterae* sp. nov.

All specimens are housed in the British Museum (Natural History) and the Geological Survey of South Africa, designated BMNH and SAS respectively.

SYSTEMATIC PALAEOONTOLOGY

Superfamily HOPLITACEAE H. Douvillé, 1890

Family **Hoplitidae** H. Douvillé, 1890

Subfamily Gastroplitinae Wright, 1952

Genus *Alopecoceras* Kennedy & Klinger gen. nov.

Type species

Alopecoceras ankeritterae gen. et. sp. nov., low Middle Albian, Zululand.

Derivation of name

Alopex (Greek) fox.

Diagnosis

Initially depressed, whorl section trapezoidal with sparse conical or bullate umbilical nodes giving rise to pairs of ribs with additional ribs intercalated; all ribs bearing conical ventral tubercles and connected across the fastigiate venter by a much thickened rib. Whorl section becomes compressed and lanceolate in later growth, venter narrowly rounded and ornament reduced to low falcoid ribs with interspaces sometimes accentuated into feeble constrictions. Suture line with moderately incised bifid elements.

Discussion

Alopecoceras closely resembles *Neogastrolites* McLearn, 1930, but is of low Middle Albian age whereas that genus, a descendant of *Gastrolites* McLearn, 1930, is of late Albian age. Because of the great intraspecific variation in *Neogastrolites* (see Reeside & Cobban 1960) it is a little difficult to make overall statements of difference, but in general *Alopecoceras* is consistently more evolute, tubercles are lower on the flank, ribs fewer and less flexuous in juveniles, the ventral ribbing thicker and less convex.

Neogastrolites typically develops a siphonal tubercle and is rostrate; neither of these features are seen in *Alopecoceras*, whilst the suture lines are more intricately subdivided.

When adult, *Neogastrolites* may become smooth and very compressed (e.g. Reeside & Cobban 1960, pl. 17 (figs 17, 22), pls 18–19), but lack the

flexuous branching ribs and feeble constrictions of *Alopecoceras*. Furthermore, these individuals have slender, feebly ornamented inner whorls: individuals of a similar degree of inflation to *Alopecoceras ankeritterae* retain strong ribs and nodes to a great size (Reeside & Cobban 1960, pl. 11 (figs 16, 20), pl. 12 (figs 11–12, 16), pl. 36 (figs 1, 5, 9–11)).

Alopecoceras can be easily separated from *Gastroplites* McLearn, 1930 (see Reeside & Cobban 1960 pls 8–9), for that genus does not possess umbilical bullae and is usually more involute.

Lemuroceras Spath, 1942, never develop strong umbilical nodes, shoulder tubercles or a fastigate venter (see illustrations in Collignon 1963).

Arcthoplites Spath, 1925 (see illustrations in Casey 1965, text-fig. 177), and *Subarcthoplites* Casey, 1954, both have strong, narrow ribs, round venters and lack tubercles, as does *Cymahoplites* Spath, 1922.

Alopecoceras shows closer similarities to *Tetrahoplitoides* Casey, 1954 (see Fig. 7H–J); both have a trapezoidal whorl, although, in the type species at least, the whorls are slender, the umbilical tubercles are bullate and not conical as in *Alopecoceras*. The venter is narrower in *Tetrahoplitoides*, flat rather than fastigate, and lacks ventrolateral tubercles.

Evolutionary origins

Alopecoceras occupies an isolated geographic position, and its evolutionary origins are far from obvious in the remaining faunas of both the South African and Madagascar Albian. C. W. Wright has, however, called our attention to its similarities to the genus *Hatchericeras* Stanton, 1901. Originally described from Patagonia, this genus was referred to the Neocomitinae Spath, 1924, in the *Treatise*, and regarded as of possibly Lower Hauterivian age. Subsequent publication by Leanza (1970) has show it to be an early Albian gastroplitinid. During middle growth (Fig. 7A–D) it differs from *Alopecoceras* very obviously in the lack of umbilical nodes and in possessing numerous flexuous ribs. There are, however, blunt thickenings of the ribs—incipient tubercles—at the ventrolateral shoulder in some species, and a broad, blunt rib crosses the venter.

Adults (Leanza 1970, fig. 31a–b) are compressed, with a rounded venter, feeble flexuous ribs and striae, plus feeble constriction-like folds. The sutures (Fig. 6C) of the two genera are also constructed on the same plan, with a similar degree of incision.

The authors would conclude, therefore, that *Alopecoceras* is an offshoot of *Hatchericeras* which has developed prominent umbilical nodes, accentuated the ventral tubercles present in some of the latter, and developed a fastigate rather than flattened venter: it is a homoeomorphous Southern hemisphere analogue of *Neogastroplites* rather than a close relative.

Occurrence

Alopecoceras is known only from the low Middle Albian of Zululand.

Alopecoceras ankeritterae gen. et. sp. nov.

Figs 1-4, 5A-B, 6, 7E-G

Holotype

BMNH C81266 from locality 35, cliff and stream sections extending over several hundred metres along the Mzinene, approximately 1 200 m north-east of the farm Amatis, north of Hluhluwe, Zululand, 27°58'03"S 32°18'31"E Mzinene Formation, Albion III.

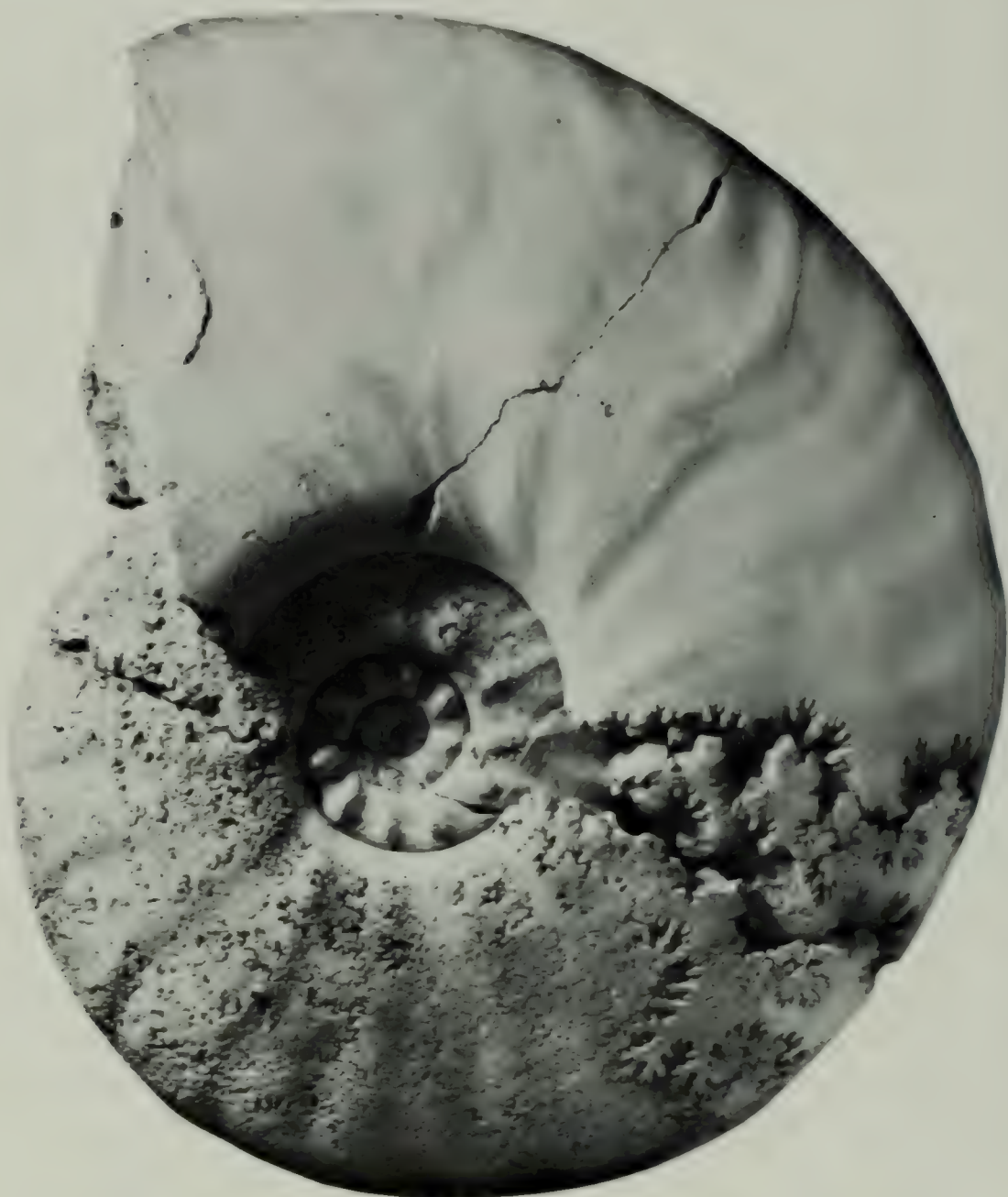


Fig. 1. *Alopecoceras ankeritterae* sp. nov. The holotype, BMNH C81266. $\times 1$.



Fig. 2. *Alopecceras ankeritterae* sp. nov. Inner whorls of the holotype, BMNH C81266. $\times 1$.

Paratypes

BMNH C81267 to C81274, SAS H54a-b, SAS A584, all from the same horizon and locality as the holotype; SAS EM152 from locality 171, on the hill slopes west-south-west of Mlambongwenya Store, Zululand, Mzinene Formation, Albian II-III, and SAS A589 from locality 53, a derelict dam site on Indambana, south of Izwehelia Farm, north of Hluhluwe, Zululand, Mzinene Formation, Albian II.

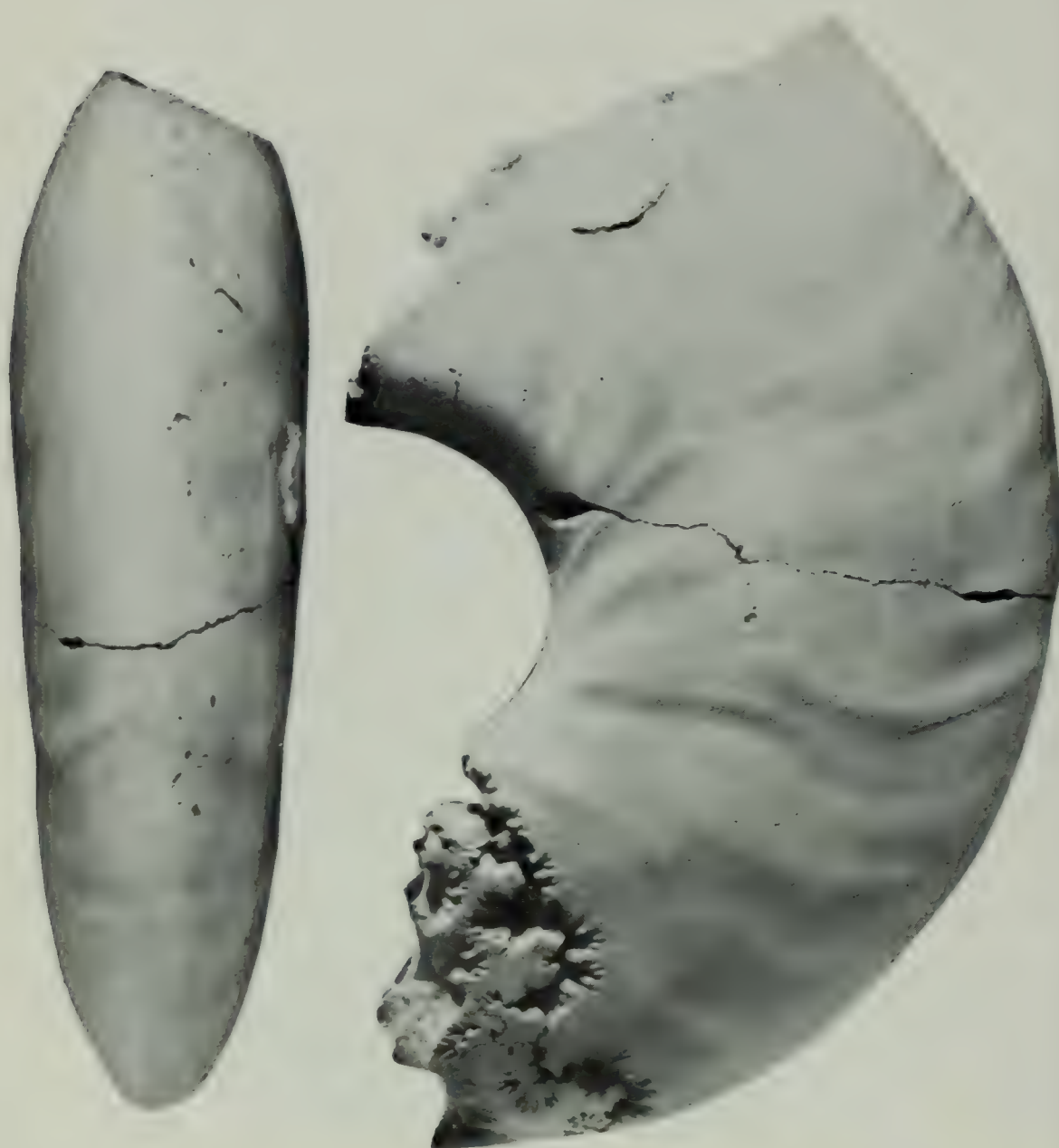


Fig. 3. *Alopecoceras ankeritterae* sp. nov. Body chamber of the holotype, BMNH C81266. $\times 1$.

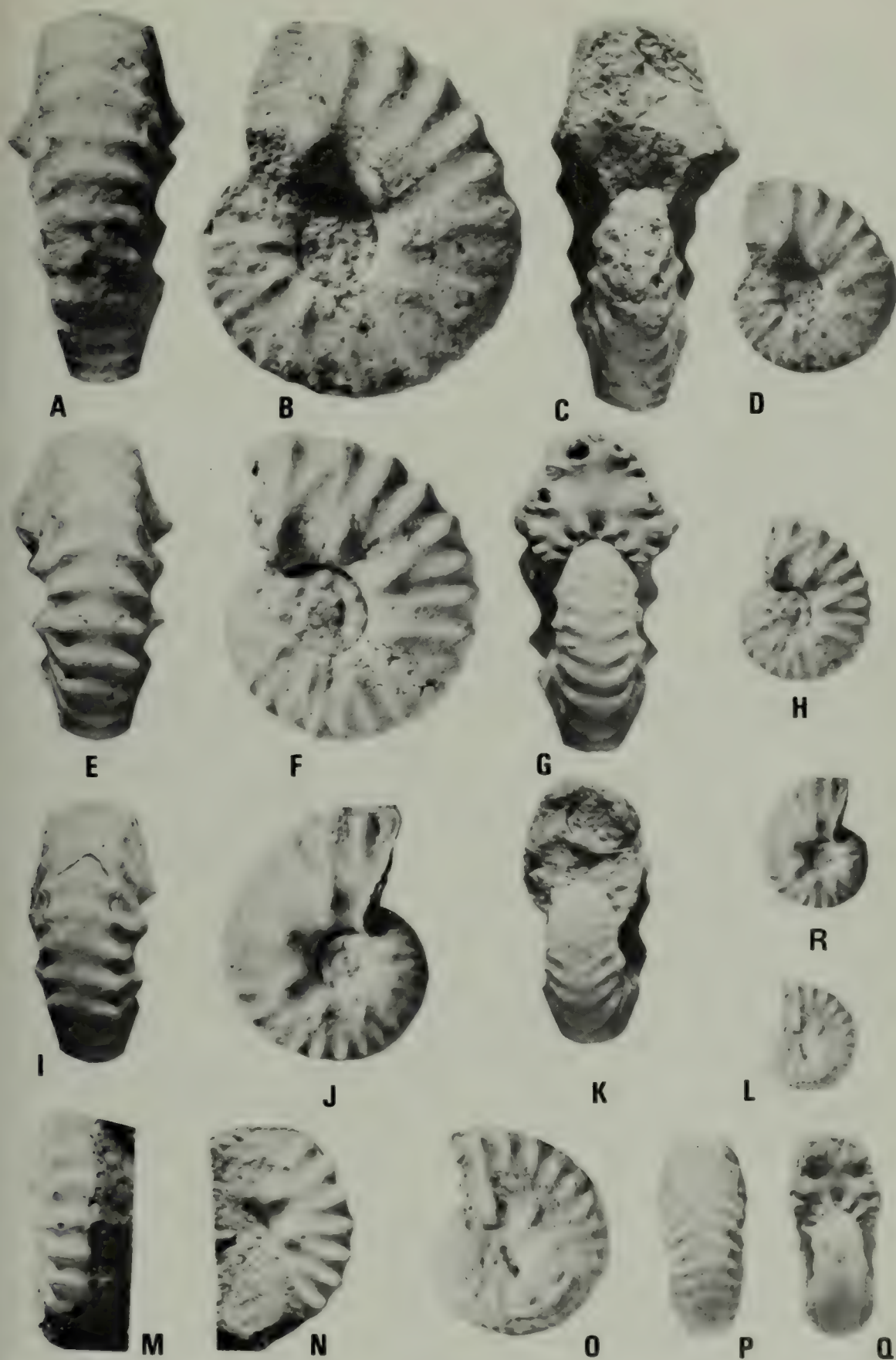


Fig. 4. *Alopecoceras ankeritterae* sp. nov. Paratypes BMNH C81267-C81271. A-C, E-G, I-K, P-R $\times 2$; D, H, L-O $\times 1$.

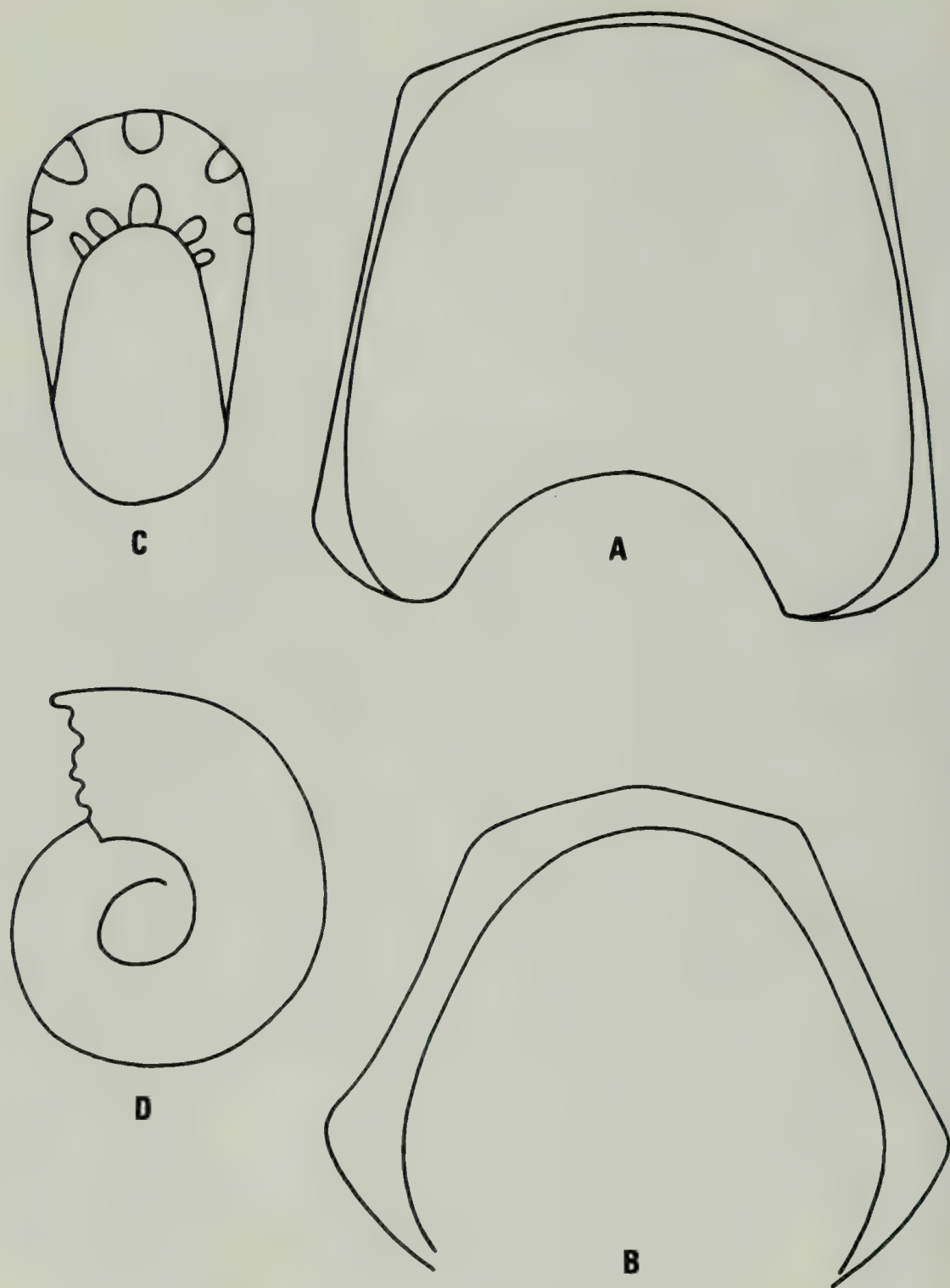


Fig. 5A-B. Whorl sections of *Alopecoceras ankeritterae* sp. nov. A. BMNH C81274. $\times 12$. B. BMNH C81268. $\times 6$. C-D. Early whorls of BMNH C81274. $\times 12$.

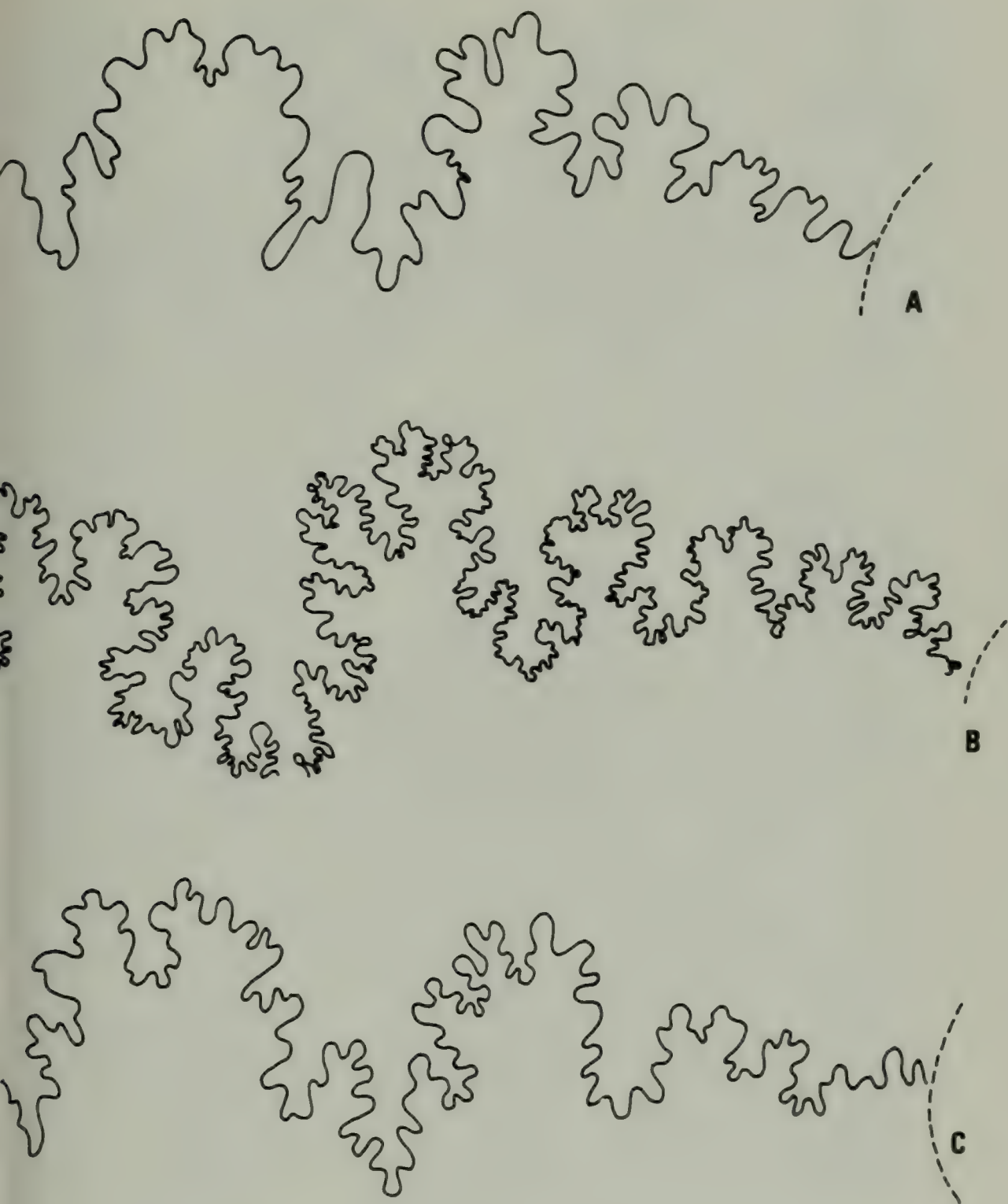


Fig. 6. A-B. *Alopoceras ankeritterae* sp. nov. External sutures of BMNH C81268, $\times 12$, and BMNH C81266, $\times 3$. C. *Hatchericeras semilaeve* Leanza. External suture of a specimen in C. W. Wright's collection from Santa Cruz, Argentine. $\times 6$.

Derivation of name

The species is named for Anke Ritter of Gauting.

Diagnosis

As for genus.

Dimensions

All dimensions are in millimetres. D = diameter, Wb = whorl breadth, Wh = whorl height, U = umbilical diameter, R = ribs per whorl.

Figures in parentheses are dimensions expressed as a percentage of diameter.

		D	Wb	Wh	Wb:Wh	U	R
Holotype							
BMNH C81266	..	137,5(100)	35(26)	61,2(45)	0,57	34,0(25)	—
	at	97,9(100)	26,4(27)	42,8(44)	0,62	24,3(25)	32
	at	67,2(100)	21,8(32)	30,0(45)	0,72	18,7(28)	—
SAS A584	41,9(100)	19,5(47)	18,5(44)	1,05	10,2(24)	21
BMNH C81267	..	25,5(100)	11,8(46)	10,5(41)	1,12	7,2(28)	26
SAS H54a	23,9(100)	11,0(46)	10,9(46)	1,01	6,0(25)	26
BMNH C81268	..	22,7(100)	10,4(46)	8,7(38)	1,19	6,3(28)	26

Description

The early developmental stages are seen in BMNH C81274. At a diameter of 3,8 mm, the juvenile shell is cadicone, the umbilicus comprising approximately 30 per cent of the diameter, with a whorl breadth to height ratio of 1,4 (Fig. 5C–D). Ornament consists of blunt, low, rounded umbilical nodes, which first appear at a diameter of *c.* 3 mm. These occur at a rate of seven per whorl up to a diameter of 6 mm, and in this interval, low, broad folds pass across the flanks and venter, although never developing into clearly delineated ribs. By 6 mm diameter, the whorl breadth to height ratio has become 1,2.

From 6 mm (Fig. 4A–R) the whorl section changes from depressed and reniform to trapezoidal. The umbilicus is shallow, and the wall slopes gently outwards. The greatest breadth is at the umbilical bullae, and the whorl breadth to height ratio is commonly reduced to 1,1. In intercostal section the outer flanks are flattened, the ventrolateral shoulders broadly rounded and the venter very broadly rounded. In costal section, the flanks are concave at mid-flank and flattened on the outer flank, and the venter fastigiate.

There are eight to ten prominent umbilical bullae per whorl, placed well out from the umbilical seam, and these give rise to groups of two or three broad ribs, weakened at mid-flank, where additional short ribs are intercalated, and recti- to feebly rursiradiate in some cases. All ribs bear a bullate to conical tubercle at the ventrolateral shoulder, and there are commonly twenty-five to twenty-eight ribs per whorl. The ribs pass across the venter with a faint convexity, broadening and diminishing in elevation over the siphonal line.

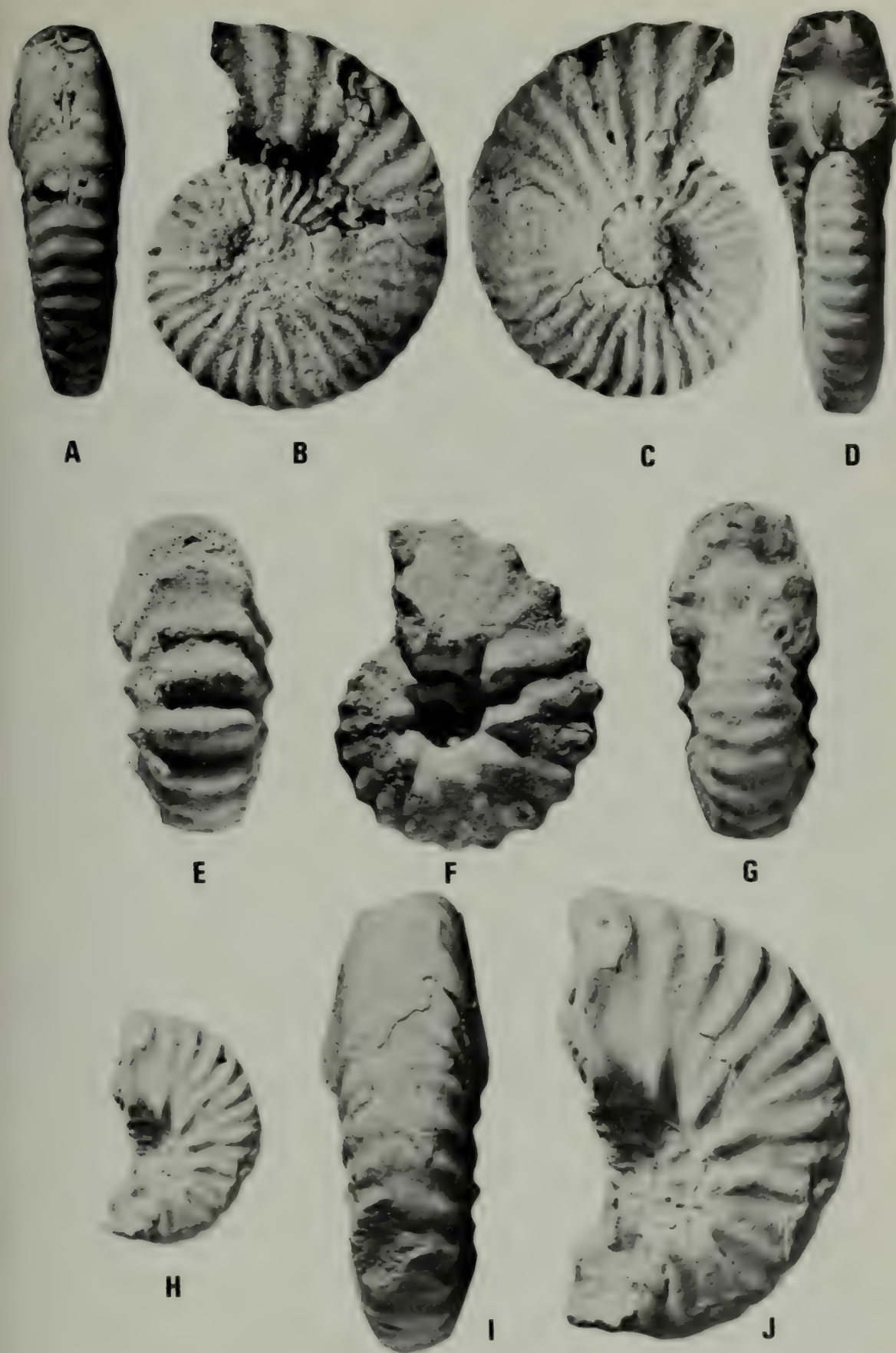


Fig. 7. A-D. *Hatchericeras semilaeve* Leanza. Inner whorls of a specimen in C. W. Wright's collection from Santa Cruz, Argentina. $\times 1$. E-G. *Alopecoceras ankeritterae* sp. nov. Paratype, SAS H93/3. $\times 1$. H-J. *Tetrahopliloides stantoni* (Anderson) cast of the holotype, from Texas Springs, Shasta County, California. H $\times 1$, I-J $\times 2$.

This general style of ornament extends to a diameter of c. 50 mm; as size increases, the whorls eventually change from depressed to compressed, the ribs coarsen, and, on the venter, become very thick (Fig. 2C). There is some variation in strength and number of ribs, bullae and whorl section at this stage, as can be seen from the figures.

The features of later growth are shown by the holotype (Figs 1–3). Here, from 50 mm onwards, all ornament declines, the ribs become low, broad and flexuous, arising in pairs from the bullae, whilst the whorl becomes compressed and lanceolate in section with a narrowly rounded venter which is crossed by ribs and has, as a result, an undulose profile.

On the mature body chamber (Fig. 3), coiling has become more evolute, with a low, outwards sloping, flattened umbilical wall. There is a somewhat abrupt umbilical shoulder and high, lanceolate whorls (whorl breadth to height ratio is 0,57 to 0,62) with a narrowly arched venter.

Ornament consists of irregular falcoid ribs and striae, arising from feeble umbilical bullae, separated by interspaces which may be strengthened into feeble, irregular constrictions.

The suture line (Fig. 6B) at maturity is moderately divided. E/L is broad and asymmetrically bifid, L broad and asymmetrically bifid. L/U₂ is large, although narrower than E/L, and asymmetrically bifid. U₂ is narrow and quite deeply divided.

Discussion

Features which separate *Alopeceras ankeritterae* from species of other genera are fully covered in comments in the generic discussion on p. 58.

Occurrence

Low Middle Albian of Zululand only.

ACKNOWLEDGEMENTS

Our best thanks are due to Mr C. W. Wright for drawing our attention to the similarities between *Alopeceras* and *Hatchericeras*, as well as providing useful discussion. We are also grateful to Dr M. R. Cooper (Oxford), Dr M. K. Howarth and Mr D. Phillips (British Museum, Natural History) and the staff of the Geological Collections, Oxford, and the South African Museum for technical assistance.

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Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Leda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierti Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

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WILLIAM JAMES KENNEDY
&

HERBERT CHRISTIAN KLINGER

CRETACEOUS FAUNAS FROM ZULULAND AND
NATAL, SOUTH AFRICA
A NEW GENUS AND SPECIES OF GASTROPLITINAE
FROM THE MZINENE FORMATION (ALBIAN)

S. H. Capetown

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KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) 2: 309-320.

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THEILE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* 4: 269-270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* 16: 269-270.

(continued inside back cover)

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UPPER CRETACEOUS SEDIMENTS FROM THE
IGODA RIVER MOUTH, EAST LONDON,
SOUTH AFRICA

By

HERBERT CHRISTIAN KLINGER
&
BRIAN E. LOCK

Cape Town Kaapstad

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By

HERBERT CHRISTIAN KLINGER

South African Museum, Cape Town

&

BRIAN E. LOCK,

The University of Southwestern Louisiana, Lafayette

(With 7 figures)

[MS. accepted 20 September 1978]

ABSTRACT

The name Igoda Formation is proposed for a sedimentary sequence consisting mainly of calcareous sandstones and arenaceous limestones exposed on the bluffs overlooking the Igoda River Mouth near East London, South Africa. The invertebrate fauna indicates a Late Cretaceous age, probably Late Campanian to Early Maastrichtian. Faunal paucity precludes detailed comparison with other areas in southern Africa, but common faunal elements occur at Lower Needs Camp (here regarded as a lateral facies equivalent of the Igoda Formation), Pondoland, Zululand, Madagascar and Angola. Affinities with Madagascar are strongest.

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INTRODUCTION

Late Cretaceous fossiliferous limestones have long been known from the eastern Cape from one of the small quarries on the farm Needs Camp (the East or Lower Quarry) near East London (Lang 1908; Woods 1908; Chapman 1916). McGowran & Moore (1971) established a probable Upper Senonian (Campanian to Maastrichtian) age for this deposit on the basis of the microfaunal content. Contrary to a report by King (1972), the second quarry at Needs Camp (the West or Upper Quarry) is excavated in limestones of Tertiary age (Lock 1973 and in preparation). Microfaunal investigations confirm this

(W. G. Siesser pers. comm.), although reworked Cretaceous material occurs in the limestones.

Until 1974 no other outcrops of Late Cretaceous marine sediments had been reported from south of the Umzamba Estuary (Pondoland, Transkei).

Mountain (1974: 19) briefly described a new fossiliferous locality less than 15 km from Needs Camp as follows: The rock occurs in a 'tiny exposure on the East London-Kidd's Beach road just west of the Goda River valley as the road climbs up on to the coastal plain. It can be seen in the present road cutting and consists of a friable limestone with abundant echinoid spines, *Ostrea* shells and gastropod casts. It is possibly Cretaceous but no one has examined the microfossils.'

Following landslides during the last few years, an extension of this occurrence became exposed in the bluffs overlooking the western shore of the lagoon at Igoda Mouth, less than a kilometre from the roadside section mentioned by Mountain (Fig. 1).

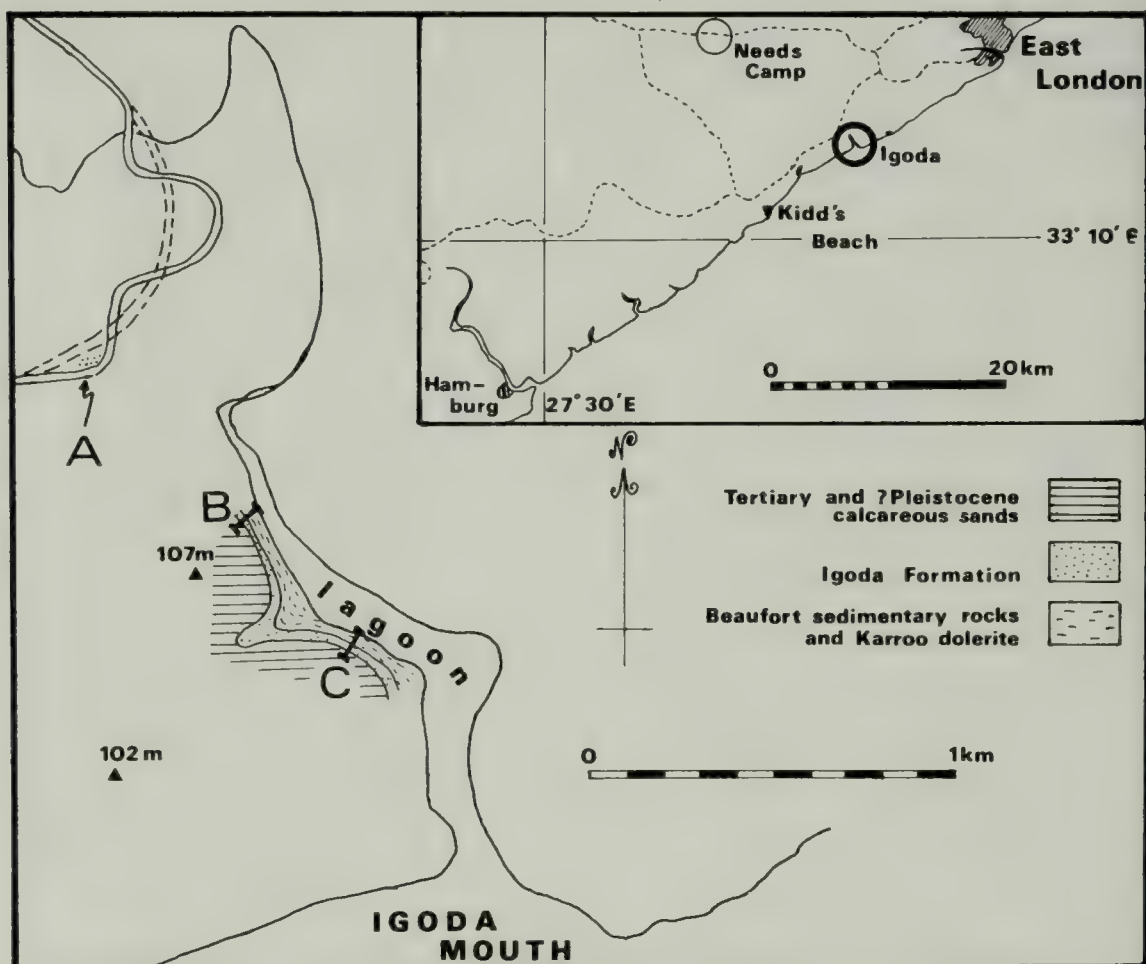


Fig. 1. Locality map, Igoda Formation. A. Roadside exposure reported by Mountain (1974); note the new road under construction. B. Type section of the Igoda Formation. C. Reference section. (See also Fig. 2.)

THE IGODA MOUTH SECTION

The succession in the new exposures is summarized in Figure 2.

The Cretaceous sequence, here named the Igoda Formation, rests unconformably on sandstones and mudstones of the Permian Triassic Beaufort Group, which have been intruded by dolerites of later Karoo age. The contact is one of some relief. The type section (sections B1, B2) is a composite one (see Fig. 1 for location and Fig. 2 for sections), and has at its base up to 50 cm of matrix-supported small-pebble conglomerate, comprising well-rounded and well-sorted brown-stained pebbles with a mean diameter of about 2 cm but with individual pebbles up to about 5 cm long. Pebble lithologies consist of vein-quartz and quartz arenites for the most part, although one pebble was a single, well-rounded crystal of orthoclase 1.2 cm long.

The matrix is an arenaceous limestone with abundant glauconite. Some shell fragments are present in this limestone matrix. The basal conglomerate passes up into a sequence of arenaceous limestones and calcareous sandstones, all with a high content of glauconite. As this section is followed up the slope, exposures become very poor, and only a few of the more resistant calcareous beds form ledges. At an altitude some 20 m above the small-pebble conglomerate, a second unconformity, at the base of the overlying Alexandria Formation (of probable Tertiary age), is reached.

The middle portion of the Igoda Formation is better exposed some 30 m to the south. In this second section a brown, small-pebble conglomerate, indistinguishable from that just described, lies at the base of a similar sequence of well-exposed glauconitic arenaceous limestones and calcareous sandstones. As in the first section, these strata are fossiliferous, yielding a shelly fauna dominated by ostreids which litter the surface. At this point, however, the calcareous sequence has a much reduced thickness of just over 7 m, and the small-pebble conglomerate overlies a 3-metre-thick sequence of white, poorly consolidated, unfossiliferous sandstone and white, small-pebble conglomerates which are in all other respects identical to the brown ones already described.

These three lithological associations are regarded as informal members, and are known as the 'white member', 'brown, small-pebble conglomerate member' and 'calcareous member' respectively.

The base of the Alexandria Formation is marked by another conglomerate consisting of much larger pebbles (up to 30 cm in diameter) mostly of Beaufort Group sandstone and siltstone. These pebbles are generally less resistant than those found in the conglomerates of the Igoda Formation. The matrix of the Alexandria Formation basal conglomerate is a coarse bioclastic limestone containing fossil gastropods, especially *Patella* sp. and *Conus* sp., usually as moulds. Glauconite is absent to rare. This unit is about 1.5 m thick and is overlain by 10 m of cross-bedded, well-indurated, coarse bioclastic limestones. Characteristically, the cross-bedding comprises a single tabular set, with seaward dips of about 25°. Above this scarp-forming unit is a considerable thickness (at least 30 m) of poorly consolidated calcareous aeolian sands.

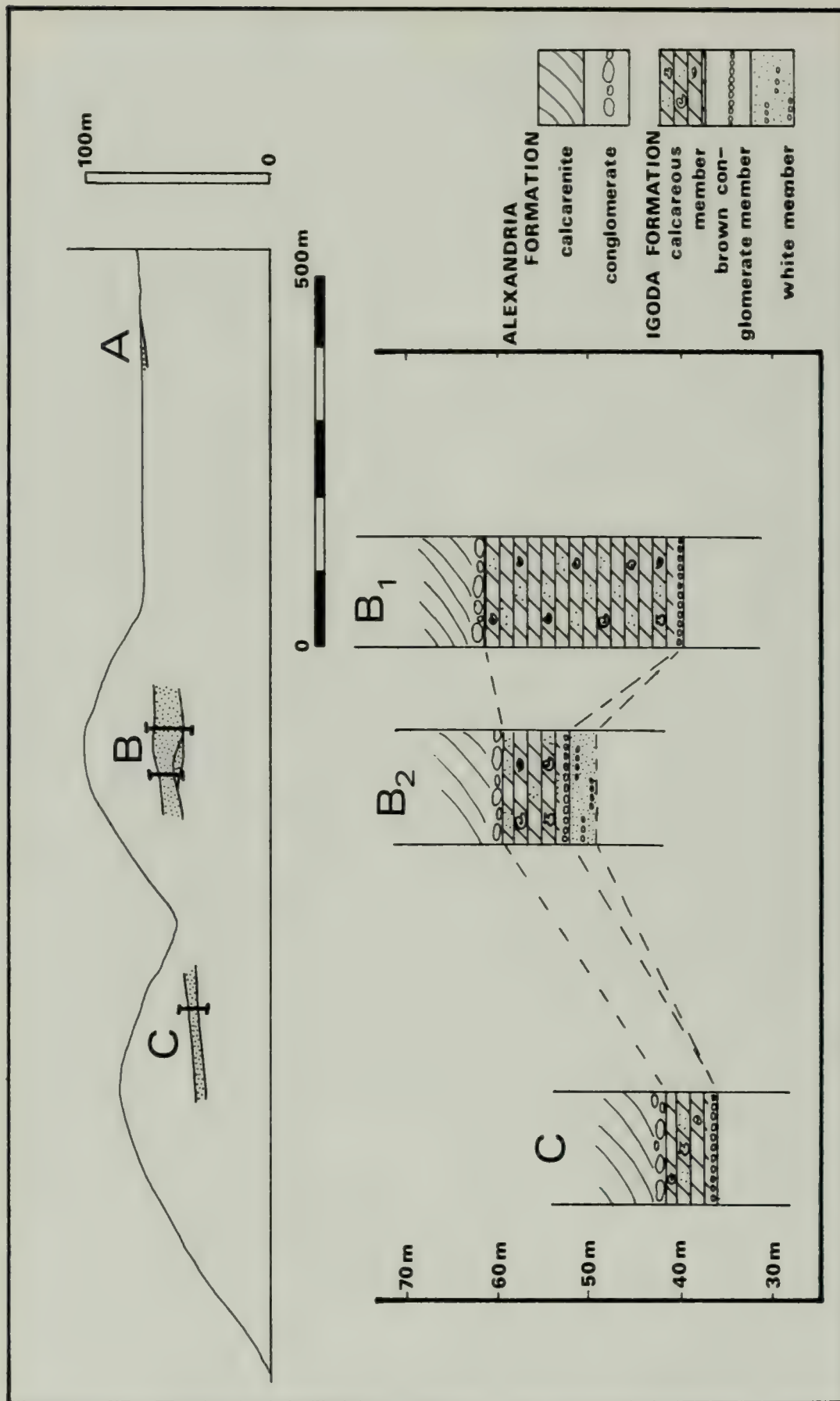


Fig. 2. Western bank of Igoda lagoon, showing distribution of outcrops described in text (above) and stratigraphic sections (below). Altitudes are in metres above lagoon water level, approximately high water mark. (See also Fig. 1.)

A second section was measured, 500 m closer to the sea (section C). Here the white member is no longer present, and the calcareous member is even further reduced in thickness (5,5 m). In other respects the sequence is similar (see Fig. 2).

THE ROAD SECTION

The original outcrop described by Mountain (1974, see above) was identified, and the adjective 'tiny' found to be very appropriate. Only a few tens of centimetres of very weathered glauconitic arenaceous limestone can be seen overlying Beaufort Group sandstones and merging upwards into soil and surface debris in the bank at the inland side of the road. The outcrop is very overgrown and easily overlooked. Broken specimens of *Rhynchostreon decussata* and *Lopha* spp., common forms in the main outcrop area, establish a correlation with the lagoon-side exposures.

At the time of the most recent visit (May 1977), roadwork was in progress for the straightening and improving of the main coastal road. Where this new road reaches the approximate altitude of Mountain's outcrop, it runs about 100 m inland of the latter, and cuts through a mass of dolerite. At the top of the cutting at this point, a few rounded pebbles of Beaufort Group sandstone in a calcareous cement were found. The size of these pebbles (20–30 cm) suggests that they are remnants of the conglomerate from the base of the Alexandria Formation. This would imply that the Igoda Formation pinches out at this point (area A on map, Fig. 1).

FAUNA AND AGE OF THE IGODA FORMATION

In comparison with the Cretaceous sediments of Zululand and Transkei (Kennedy & Klinger 1975 onwards), the invertebrate fauna of the Igoda Formation is meagre and poorly preserved. Bivalves are the commonest group, especially the ostreid forms, which have been preserved by virtue of their unique shell mineralogy, followed by brachiopods, baculitid ammonites, echinoids, and rare, normally coiled, ammonites, in that order of abundance.

At present, the material in the authors' collections is too scant to merit formal description and discussion, but a preliminary examination of the fauna has revealed the presence of the following faunal elements:

FORAMINIFERA

Textularia sp.

COELENTERATA

'*Caryophyllia*' cf. *arcotensis* Forbes (Fig. 3)

ECHINODERMATA

Unidentifiable cidarid with uniserial pore pairs (Fig. 4B)

Crinoid stem ossicles of *Pentacrinus* type (Fig. 4A)

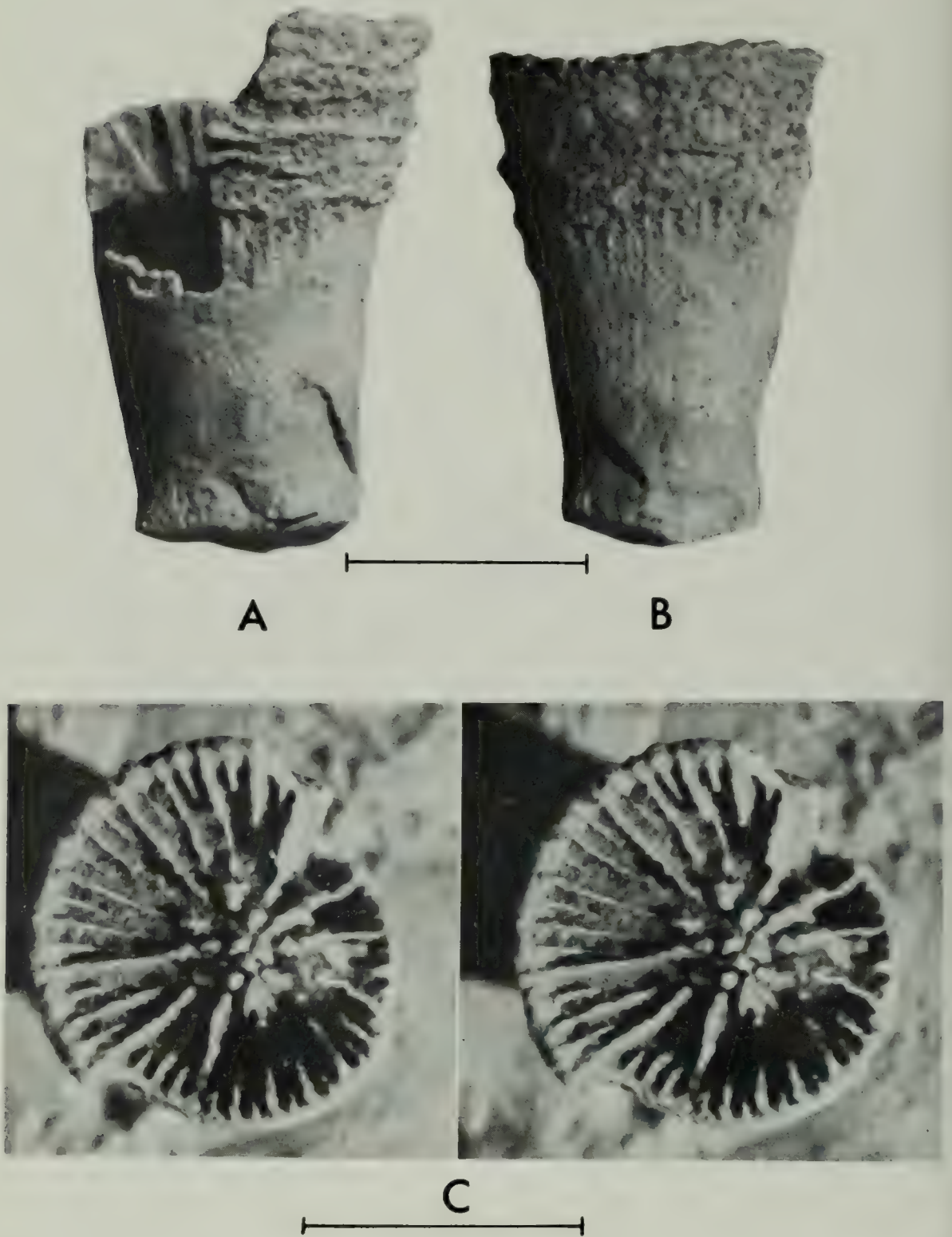


Fig. 3. '*Caryophyllia*' *arcotensis* Forbes (Geology Department, Rhodes University.)
A-B. Lateral view. Scale bar 0,5 cm long. C. Dorsal view, stereopair. Scale bar 0,5 cm long.

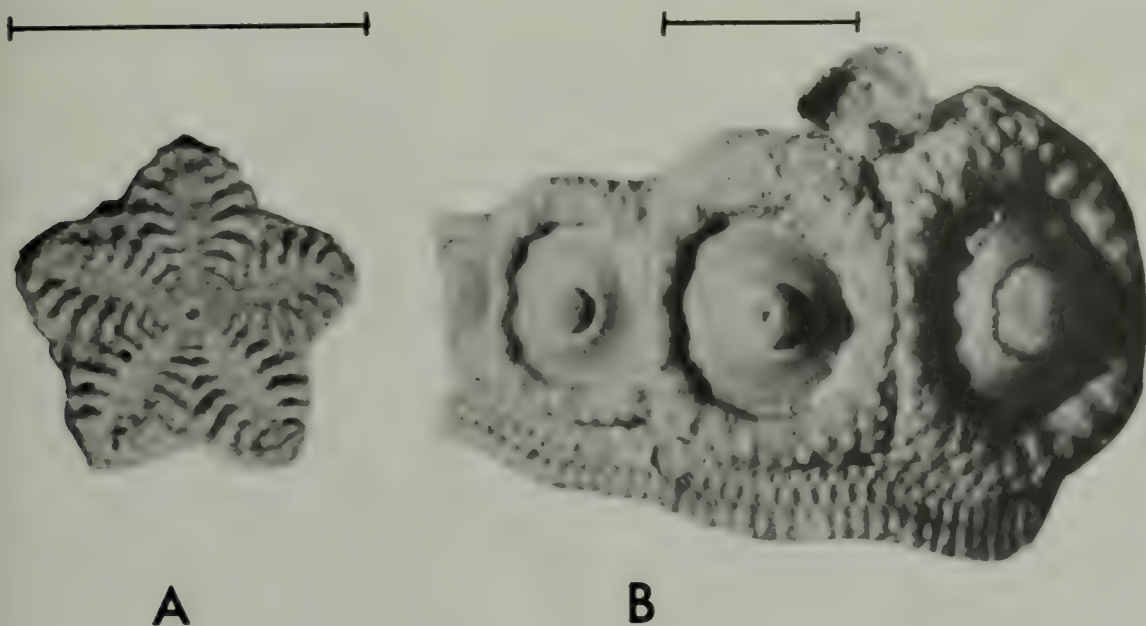


Fig. 4. A. Crinoid stem ossicle of the *Isocrinus* type. B. *Cidaris* sp. indet.
Scale bars 0,5 cm long.

MOLLUSCA—CEPHALOPODA

- Baculites subanceps* Haughton (Fig. 5)
Eupachydiscus? sp. (Fig. 6)
 Pachydiscid sp. indet (compressed)
Saghalinites sp. cf. *S. cala* (Forbes) (Fig. 7A–B)

MOLLUSCA—GASTROPODA

- Turritella* (*Zaria*) cf. *T. (Z.) besairiei* Basse

MOLLUSCA—BIVALVIA

- Rhynchostreon decussata* (Goldfuss)
Lopha (*Actinostreon*) *schnaebelei* Basse (Fig. 7C–H)
 'Trigonia' sp.
Spondylus douvillei Basse
Panopea cf. *orientalis* (Forbes)
 'Inoceramus' spp.

BRYOZOA

- cf. *Ceriopora micropora* Goldfuss
 'Membranipora' cf. *plebicola* Brydone

BRACHIOPODA

- cf. *Terebratulina relict*a Stoliczka
 cf. *Terebratula manuaensis* Muir-Wood
 cf. *Rhynchonella natuans* Stoliczka
Eolacazella affine (Bosquet)



Fig. 5. *Baculites subanceps* Haughton. A, C. SAM-PCI5721. $\times 1,2$. B. SAM-PCI5723. $\times 1,0$. D. SAM-PCI5728. $\times 1,0$. E-H. SAM-PCI5906. $\times 1,0$. I-L. SAM-PCI5720. $\times 1,0$.



Fig. 6. *Eupachydiscus*? sp. indet. SAM-PCI5719. $\times 1,0$.

Of the species identified, only a few can be used for accurate dating of the Igoda Formation.

Baculites subanceps s.s. has been firmly dated as Late Campanian in Angola (Howarth 1965), whilst the Pacific subspecies *B. anceps pacificus* occurs in the Late Campanian of Japan and California. *Saghalinites* ranges from the Santonian to Maastrichtian stages of the Late Cretaceous (Kennedy & Klinger 1977). *S. cala*, which the Igoda specimen resembles most, ranges from Campanian IV to Maastrichtian II (*sensu* Kennedy & Klinger 1975) in Zululand but is also known to occur in slightly older sediments in Pondoland (Transkei)

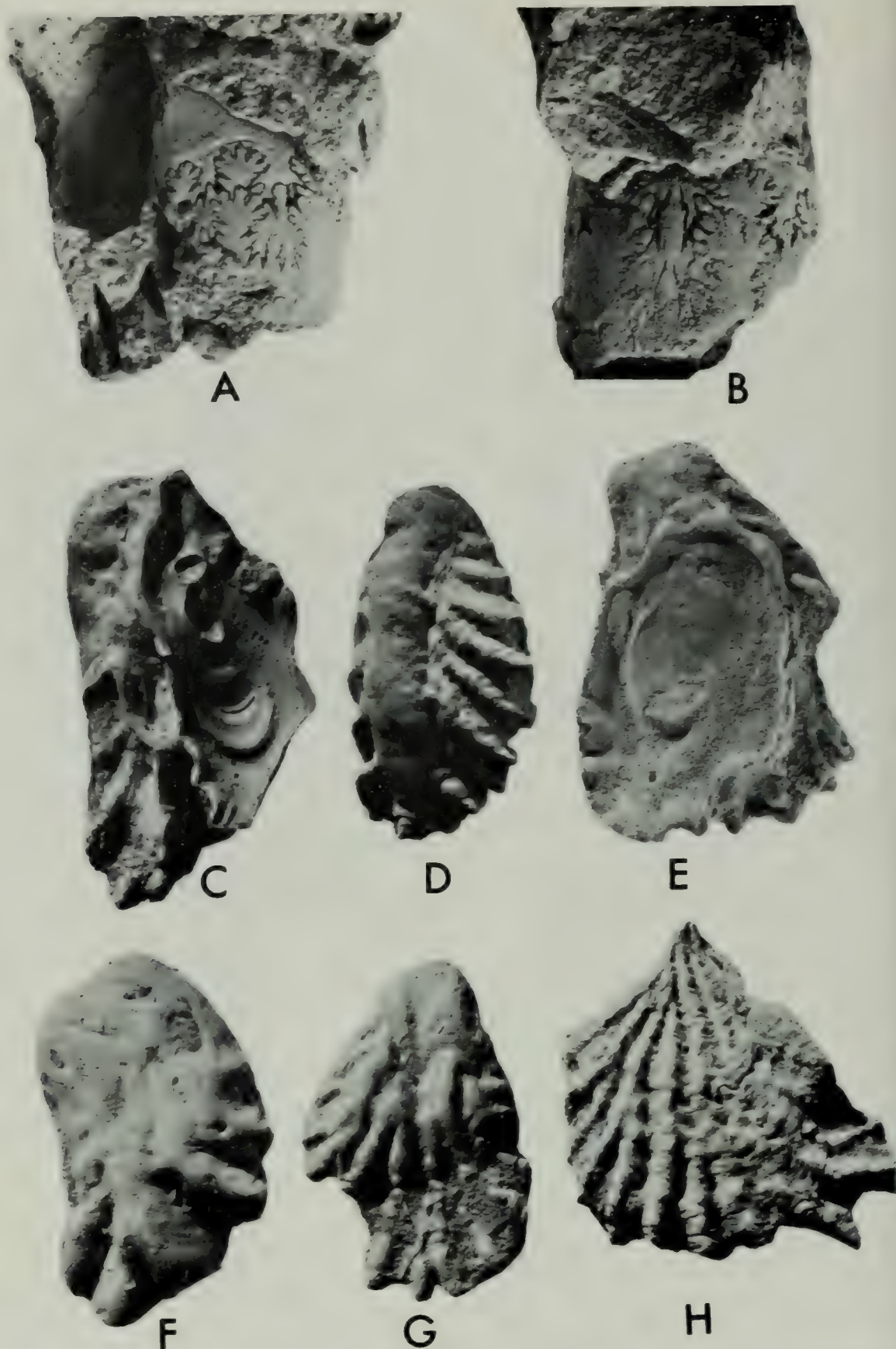


Fig. 7. A-B. *Saghalinites* sp. cf. *S. cala* (Forbes). C-H. *Lopha* (*Actinostreon*) *schnaebelei* (Basse). C. SAM-PCI5773. $\times 1,0$. D. SAM-PCI5749. $\times 1,0$. E. SAM-PCI5736. $\times 1,0$. F. SAM-PCI5750. $\times 1,0$. G. SAM-PCI5752. $\times 1,0$. H. SAM-PCI5744. $\times 1,0$.

(Middle Santonian–Lower Campanian) and southern India (Santonian or Campanian). The ammonite genus *Eupachydiscus* is typically Late Cretaceous, ranging from Coniacian to Maastrichtian, but the Igoda material is too poorly preserved for specific identification.

Ceripora micropora Goldfuss has been described from the type locality of the Maastrichtian stage, but is also common in the Santonian and Campanian. *M. plebicola* is from the Maastrichtian.

Eolacazella affine (Bosquet) occurs in the Maastrichtian of Western Europe, and was also found at the Lower Needs Camp Quarry now dated as Upper Campanian/Lower Maastrichtian by McGowran & Moore (1971).

These data all seem to suggest an age of Campanian/Maastrichtian for the Igoda Formation with only a slight possibility of Santonian elements present.

COMPARISON WITH OTHER AREAS IN SOUTHERN AFRICA

The nearest onshore sediments of similar age occur at the Lower or Eastern Quarry at Needs Camp. *Eolacazella affine* occurs at both the Igoda River Mouth and at Lower Needs Camp, thus suggesting the two outcrops to be temporal equivalents, though of different lithologies. In places, the outcrops at Lower Needs Camp consist virtually of bryozoan limestone only. Exposures of similar lithologies have since been found by one of the authors (H. C. K.) in roadside excavations approximately half-way between the Upper and Lower Quarries, illustrating that the Lower Needs Camp lithology has a much greater aerial extent than previously suspected, and may yet prove to be a mapable unit to conform with the requisites for formal recognition as a separate Formation by the South African Committee for Stratigraphy.

The Lower Needs Camp sediments probably grade laterally into the slightly deeper water facies of the Igoda Formation, but outcrops connecting the two areas are, as yet, unknown.

Along the east coast of southern Africa, the closest Senonian sediments occur at the Umzamba Estuary (Transkei), which have been firmly dated as Mid-Santonian to Lower Campanian (Klinger & Kennedy 1977). Rare *Saghalinites cala* in the Umzamba Formation are comparable with *Saghalinites* sp. in the Igoda Formation.

The closest, and thus far only known, onshore Upper Campanian/Lower Maastrichtian sediments on the east coast of southern Africa occur in the False Bay/St Lucia region of Zululand (Kennedy & Klinger 1975). Here *Saghalinites cala* occurs quite frequently with *Nostoceras* sp. and *Eubaculites* sp. in the Upper Campanian and Lower Maastrichtian respectively. *S. cala* appears to be the only identifiable faunal element in common between the two areas. Lower Maastrichtian sediments are known from Cheringoma further north in Mozambique, but to date only poorly-preserved *Eubaculites* species are known (Crick 1923).

Much further north, the Campanian and Maastrichtian faunas of Maintirano, Madagascar, as described by Basse (1931), strongly resemble those from

Igoda especially as far as the thick-shelled ostreid forms are concerned, and to a lesser extent with the Late Senonian fauna of the east coast Province of Vatomandry described by Cottreau (1922), which is characterized by the paucity of ammonites, similar to the Igoda Formation.

Towards the southern and western coast, the closest sediments of comparable age are found in the off-shore Alphard Group between Cape St Francis and Cape Recife (Klinger *et al.* in prep.). Here, however, the dominant faunal element is *Eubaculites latecarinatus* indicative of Early Maastrichtian age. No macrofossils are common to both outcrops.

From here westwards, the first known Cretaceous on-shore sediments occur near Bogenfels (South West Africa) (Klinger 1977), but these have been dated definitely as Cenomanian, although some doubt still exists as to whether Senonian strata are present on-shore or not.

The closest comparable deposits occur at Carimba in Angola, the type area of *Baculites subanceps*, the latter being the only faunal element in common between Igoda and Angola. The Cretaceous sediments at Carimba have been firmly dated as Late Campanian by Howarth (1965).

SUMMARY

The name Igoda Formation is proposed for a sedimentary sequence consisting mainly of calcareous sandstones and arenaceous limestones exposed on the bluffs overlooking the Igoda River Mouth. The Formation is informally divided into 'white member', 'brown, small-pebble conglomerate member' and 'calcareous member'.

In comparison with the Cretaceous sediments of Natal and Transkei, the Igoda fauna is meagre, consisting mainly of thick-shelled ostreid bivalves, followed by brachiopods, baculitid ammonites, echinoids, and rare, normally coiled ammonites, in that order of abundance.

These faunas point to an age of Late Campanian to Early Maastrichtian.

Due to the paucity of the faunas, comparisons with other temporally equivalent areas are tenuous. The Lower Needs Camp Quarry deposits are of similar age, and probably represent a shallower water and more restricted lateral facies equivalent of the Igoda Formation. *Saghalinites* sp. cf. *cala* connects the Igoda Formation to the Cretaceous deposits on the east coast of southern Africa at the Umzamba Estuary and in the False Bay/Lake St Lucia region of Zululand.

As far as the abundance of thick-shelled ostreids and relative scarcity of ammonites is concerned, the Cretaceous deposits of Maintirano and Vatomandry in Madagascar show greatest affinity, but this should probably be ascribed to the depositional environment rather than to more favourable migration routes.

On the west coast of southern Africa, comparable deposits occur at Carimba in Angola which provide a definite date for *Baculites subanceps*, i.e. Late Campanian.

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6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierti Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

- The Figures, Maps and Tables of the paper when referred to in the text
e.g. '... the Figure depicting *C. namacolus* ...'; '... in *C. namacolus* (Fig. 10) ...'
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e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene
- Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as

'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

HERBERT CHRISTIAN KLINGER

&

BRIAN E. LOCK

UPPER CRETACEOUS SEDIMENTS FROM THE
IGODA RIVER MOUTH, EAST LONDON,
SOUTH AFRICA

S-H-Cape Town
VOLUME 77 PART 6

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FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* 74: 627-634.

KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) 2: 309-320.

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THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Sud-Afrika* 4: 269-270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* 16: 269-270.

(continued inside back cover)

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CRETACEOUS FAUNAS FROM ZULULAND
AND NATAL, SOUTH AFRICA
THE AMMONITE SUPERFAMILY
HAPLOCERATACEAE ZITTEL, 1884

By
WILLIAM JAMES KENNEDY
&
HERBERT CHRISTIAN KLINGER

Cape Town Kaapstad

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SOUTH AFRICA
THE AMMONITE SUPERFAMILY HAPLOCERATACEAE ZITTEL, 1884

By
WILLIAM JAMES KENNEDY
Geological Collections, University Museum, Oxford
&
HERBERT CHRISTIAN KLINGER
South African Museum, Cape Town

(With 20 figures)

[MS. accepted 18 October 1978]

ABSTRACT

Representatives of the superfamily Haplocerataceae Zittel, 1884, are locally common in rocks of Barremian age in northern Zululand, where *Sanmartinoceras* (*Sanmartinoceras*) *africanum* sp. nov. occurs at all stages of development from larval shells to discs which are still septate at a diameter of 120 mm, and represent the largest known specimens of the genus. *Sanmartinoceras* (*Theganeceras*) *nodosum* sp. nov., of Lower Aptian age, *Sanmartinoceras* (*Sinzovia*) *trautscholdi* (Sinzow), and an *Aconeceras* sp. of Upper Aptian age are other representatives of the Aconeceratidae, whilst the Binneyitidae are represented by specimens of *Borissiakoceras* of Middle Cenomanian age. In addition to systematic descriptions, the problems of recognizing dimorphism in these genera are discussed, and certain resultant taxonomic problems noted, and an annotated list of species referred to the two families is included.

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INTRODUCTION

The Haplocerataceae are the longest ranging of the Ammonitina, first appearing in the Middle Jurassic (Bajocian) and ranging to the Upper Cretaceous (Coniacian). As Casey has noted, two broad morphologies recur within the superfamily: firstly, smooth platycones, typified by the Haploceratidae and Binneyitidae, and secondly, variously ribbed or strigate oxycones with entire or

crenulate keels, typified by the Oppeliinae, Strigoceratidae and Aconeceratidae (Casey 1961a: 118). In the Cretaceous of Zululand both groups are represented, in the Upper Barremian and Aptian the Aconeceratidae are not uncommon at some levels, whilst the Binneyitidae occur as a great rarity in rocks of Middle Cenomanian age. Although only a few species are represented in the authors' collections, they are of some significance, for their specimens of Aconeceratidae allow, for the first time, the description of the detailed ontogeny of the widely occurring genus *Sanmartinoceras* Bonarelli, 1921, as well as clarifying some aspects of its stratigraphic distribution, whilst the present records of the binneyitid *Borissiakoceras* extend the known distribution of the group.

The following species are described below: *Aconeceras* sp., compared to *A. walshense* (Etheridge); *Sanmartinoceras* (*Sanmartinoceras*) *africanum* sp. nov.; *Sanmartinoceras* (*Theganeceras*) *nodosum* sp. nov.; *Sanmartinoceras* (*Sinzovia*) *trautscholdi* (Sinzow); and *Borissiakoceras* sp.

To this is added an annotated list of genera, subgenera and species referred to the two families.

LOCATION OF SPECIMENS

The following abbreviations are used to indicate the repositories of the material studied:

- BMNH British Museum (Natural History), London
- GSM Institute of Geological Sciences, London
- MNHP Muséum d'Histoire Naturelle, Paris
- OUM Oxford University Museum, Oxford
- SAM South African Museum, Cape Town
- SAS South African Geological Survey, Pretoria

FIELD LOCALITIES

Details of localities mentioned in the text are given by Kennedy & Klinger (1975); fuller descriptions of sections are deposited in the Palaeontology Department of the British Museum (Natural History), London; Geological Survey, Pretoria; and South African Museum, Cape Town.

DIMENSIONS OF SPECIMENS

All dimensions given below are in millimetres:

D = diameter, Wb = whorl breadth, Wh = whorl height, U = umbilical diameter.

Figures in parentheses are dimensions as a percentage of the total diameter.

SUTURE TERMINOLOGY

The suture terminology of Wedekind (1916), recently reviewed and discussed by Kullman & Wiedmann (1970) is followed here:

Is = Internal lobe with septal lobe, U = Umbilical lobe, L = Lateral lobe, E = External lobe.

SYSTEMATIC PALAEOLOGY

Phylum **MOLLUSCA**

Class CEPHALOPODA Cuvier, 1797

Subclass AMMONOIDEA Zittel, 1884

Order AMMONITIDA Zittel, 1884

Suborder AMMONITINA Zittel, 1889

Superfamily HAPLOCERATACEAE Zittel, 1884

Family **Aconeceratidae** Spath, 1923*Discussion*

The Aconeceratidae Spath, 1923, is a group of small to medium-sized, compressed, involute, commonly oxycone ammonites with flat or convex sides and a fastigiate to keeled venter. Ornament consists of weak to strong flexuous, commonly biconvex ribs and growth striae and a keel which may be minutely crenulate.

The following genera and subgenera have been placed in the family:

Genus *Protaconeceras* Casey, 1954, Hauterivian

Genus *Aconeceras* Hyatt, 1903, Barremian to Lower Albian

Genus *Sanmartinoceras* Bonarelli, 1921 (in Bonarelli & Nagera 1921),
Barremian to Lower Albian

Subgenus *Sanmartinoceras* s.s., Barremian to Aptian

Subgenus *Sinzovia* Sazonova, 1958, Aptian

Subgenus *Theganeceras* Whitehouse, 1926, Lower Aptian

Genus *Doridiscus* Casey, 1961, Aptian

Genus *Nothodiscus* Casey in Collignon, 1962, Aptian

Genus *Gyaloceras* Whitehouse, 1927, Upper Aptian.

Aconeceratids have a wide geographic distribution extending from Greenland to Antarctica, although their occurrence is sporadic. In Europe at least, they occur in enormous numbers in some clay facies as in southern France, where the blue marls of the Fosse Vocontienne yield thousands of *Aconeceras* and Casey (1961b: 122) regarded them as an open sea group which invaded the neritic zone only in periods favourable for their growth. As will be seen below, however, their local abundance in carbonaceous nearshore sandstones of the South African Barremian is scarcely compatible with such a generalization.

The Haplocerataceae as a whole are characterized by striking dimorphism (Makowski 1962, Callomon 1963, Kennedy & Cobban 1976 with references), but within the Aconeceratidae our knowledge is such that it remains most difficult to recognize dimorphic pairs. In *Aconeceras* itself, the many hundreds of specimens from the French Aptian examined are all pyritic phragmocones and it would appear that juveniles, at least, are most difficult to split into dimorphs, as Palframan (1969) found in some Jurassic haploceratids. The authors do know, however, of a few specimens referable to the family in which

apertures are preserved: the original material of *S.* (*Sanmartinoceras*) *groenlandicum* Rosenkrantz, 1934 (in Bøgvad & Rosenkrantz), illustrated here as Figure 1A–C, is an obvious microconch with prominent lappets and a rostrum. Equally, *Gyaloceras smithi* Whitehouse, 1927, appears to be a female or macroconch. The specimen is reproduced here as Figure 2A. In most cases, however, the shell ornament of aconeceratids (as opposed to apertural form) gives little clue to dimorphism and a markedly biconvex growth line, indicating a long rostrum and blunt lappets, occurs, in the present material at least, in both small and large (if not mature specimens). The authors would, however, suggest that the presence of a strong spiral depression may indicate the possible presence of a long lappet (Figs 1A–B, 5C). The topic is returned to below under the discussion of *Sanmartinoceras*.

Genus *Aconeceras* Hyatt, 1903

Type species

Ammonites nisus d'Orbigny, 1841.

Discussion

Aconeceras is represented by a single, poor specimen from the Aptian of Zululand; in consequence the reader is referred to Casey's (1961*b*: 123) extensive remarks on the genus.

Occurrence

The genus ranges from Barremian to Lower Albian and is widely distributed from western Europe and the U.S.S.R. to east Africa, Madagascar, Nepal, Antarctica and eastern Australia.

Aconeceras sp.

Material

One specimen only, BMNH C80002, from the Makatini Formation, Aptian III, locality 166, Mfongosi Spruit, northern Zululand.

Description

The specimen is an external mould of an oxycone individual with an original maximum whorl height of over 20 mm. Coiling is very involute with a small, pit-like steep-sided umbilicus. The whorl section is high, compressed with the greatest breadth well below mid-flank. The flanks are distinctly flattened and the venter fastigate.

The specimen is somewhat worn and there is no obvious trace of ornament preserved.

Discussion

Although poorly preserved, this specimen is clearly referable to the genus *Aconeceras*. Amongst described species it is perhaps to be compared with the

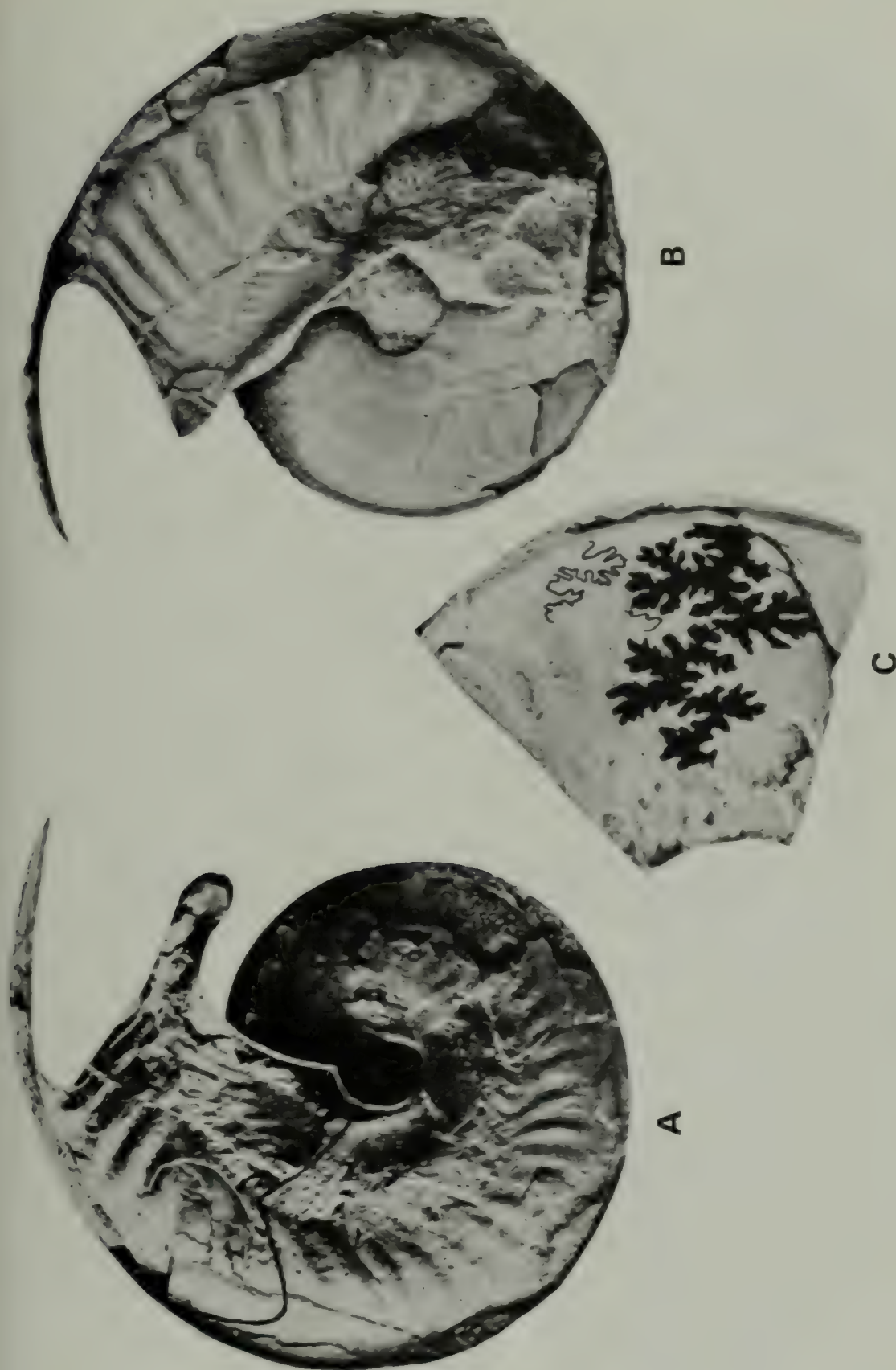


Fig. 1. *Sanmartinoceras (Sanmartinoceras) groenlandicum* Rosenkrantz, 1934. Copy of Bøgvad & Rosenkrantz (1934). $\times 2$.

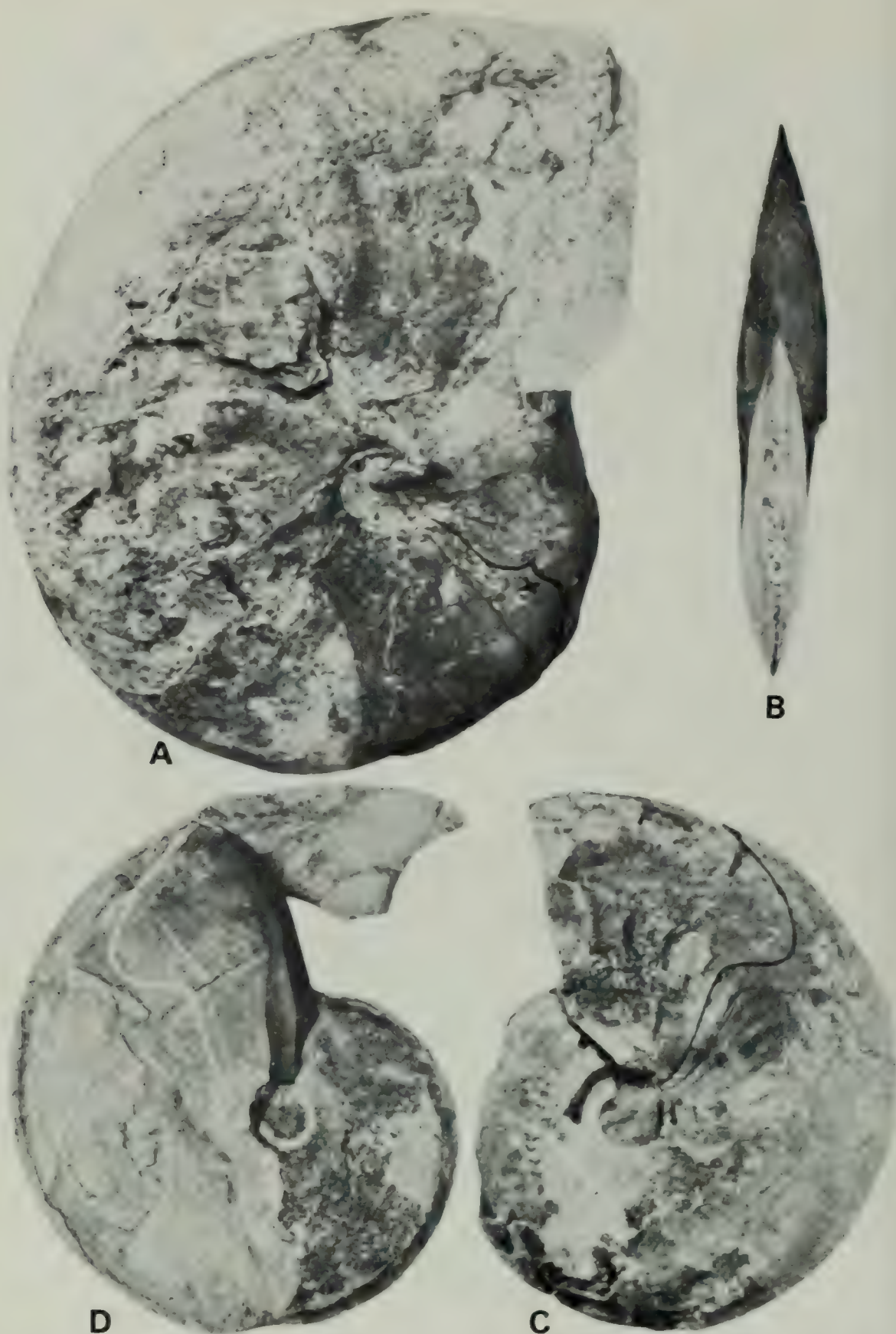


Fig. 2. A. *Gyaloceras smithi* Whitehouse, 1926. B-D. *Aconeceras walshense* (Etheridge), 1892.
After Whitehouse (1926, 1927a). $\times 1$.

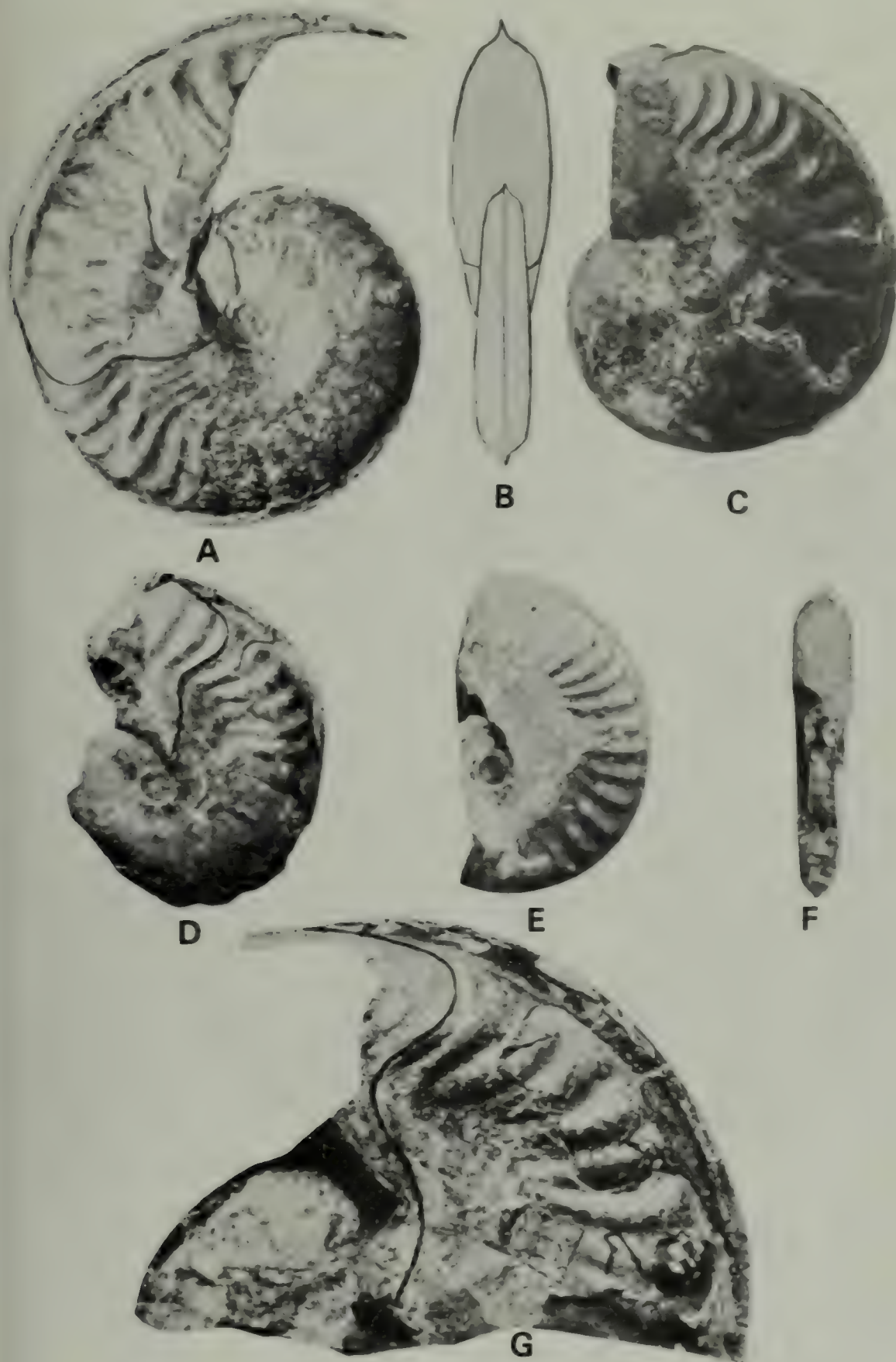


Fig. 3. A-C. *Sanmartinoceras* (*Sanmartinoceras*) *fontinale* (Hudleston), 1890.
D-G. *Sanmartinoceras* (*Sanmartinoceras*) *olenae* (Tenison-Woods), 1883. After Whitehouse
(1927a). ×1.

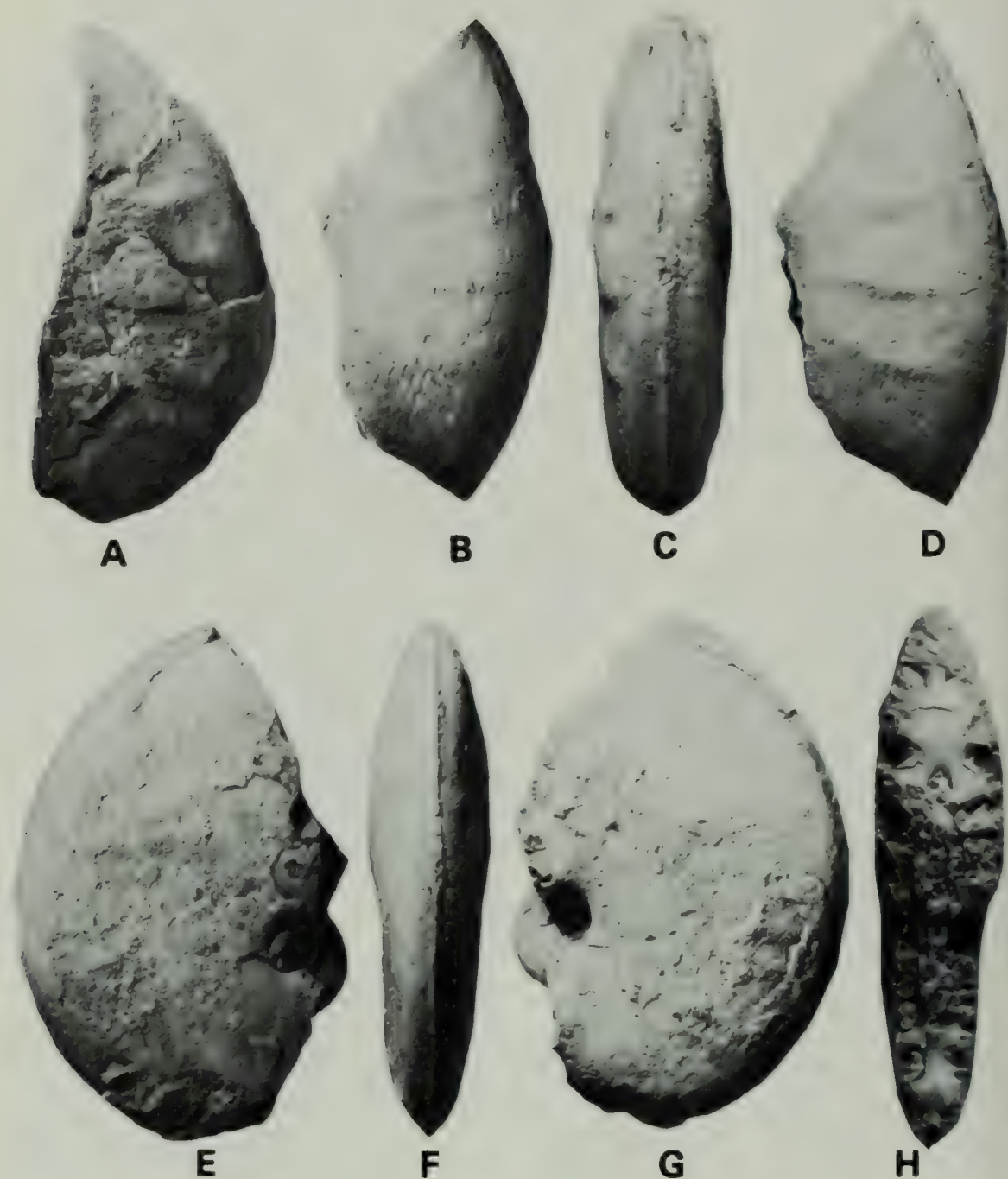


Fig. 4. *Sanmartinoceras* (*Sanmartinoceras*) *africanum* sp. nov., paratypes.
A. SAS H54/41/e. B-D. BMNH C79988. E-H. BMNH C79982. $\times 1$.

Australian *Aconeceras walshense* (Etheridge) (see Whitehouse 1927a: 114, pl. 16 (figs 2–3); text-figs 1, 6–7) (Fig. 2B–D herein).

Occurrence

Upper Aptian of Zululand.

Genus *Sanmartinoceras* Bonarelli, 1921 (in Bonarelli & Nagera 1921)

Type species

Sanmartinoceras patagonicum Bonarelli, 1921 (in Bonarelli & Nagera 1921).

Diagnosis

Stout oxycones, initially smooth, with falciform striae and ribs, the latter weak on the inner flank, sometimes bunched, and strengthening into distinctive concave ribs on the outer flank. Keel finely denticulate.

Discussion

Sanmartinoceras was originally based upon crushed specimens from the Aptian of Lago San Martin, Argentina. Leanza (1970, text-fig. 14) (see Fig. 5A–B herein) has figured uncrushed topotypes, whilst Howarth (1958) and Thomson (1974) have figured other material from the sub-Antarctic Islands. Specimens are illustrated here as Figure 5C–D. Specimens of *S. patagonicum* with apertures preserved are unknown, but Rosenkrantz (in Bøgvad & Rosenkrantz 1934: 20, pl. 4 (fig. 3), pl. 5 (figs 1–5)) figured a species, *S. groenlandicum* Rosenkrantz, with a distinctive rostrum and lappets. These features, indicative of a micro-conch, have been incorporated into the generic diagnosis. Examination of these examples shows that the lateral lappets are associated with a distinct spiral groove (Fig. 1A–B). In the Antarctic specimens (Fig. 5C–D) similarly sized individuals show this groove developed to varying degrees at the same diameter, and the authors suspect it may prove a criterion for differentiation of immature males and females at similar diameters, in the type species at least. In the case of Australian *Sanmartinoceras* the problem is even more tantalizing. Whitehouse (1926; 1927a) described four aconeceratids from the Aptian of Walsh River. Two, *Sanmartinoceras fontinale* (Hudleston) (Fig. 3D–G, 7A–H) and *S. olenae* (Tenison-Woods) (Fig. 3A–C) have strong falcoid ribs and prominent rostra. The others are very feebly ornamented. *Aconeceras walshense* (Etheridge) (Fig. 2B–D) has falcoid growth striae, whilst *Gyaloceras smithi* Whitehouse (Fig. 2A) has an inflated whorl and fastigiate venter. The authors strongly suspect that these species are dimorphs but again cannot resolve the problem fully.

Within *Sanmartinoceras*, three subgenera have been recognized. In addition to *Sanmartinoceras sensu stricto*, *Theganeceras* Whitehouse, 1926, was treated as a subgenus by both Wright (1957) and Casey (1961b). Only three species, *S. (T.) falcatum* (von Koenen) (Fig. 6I–J) *S. (T.) scalatum* (von Koenen) (Fig. 6H) from the Lower Aptian of northern Germany, and *S. (T.) grande*

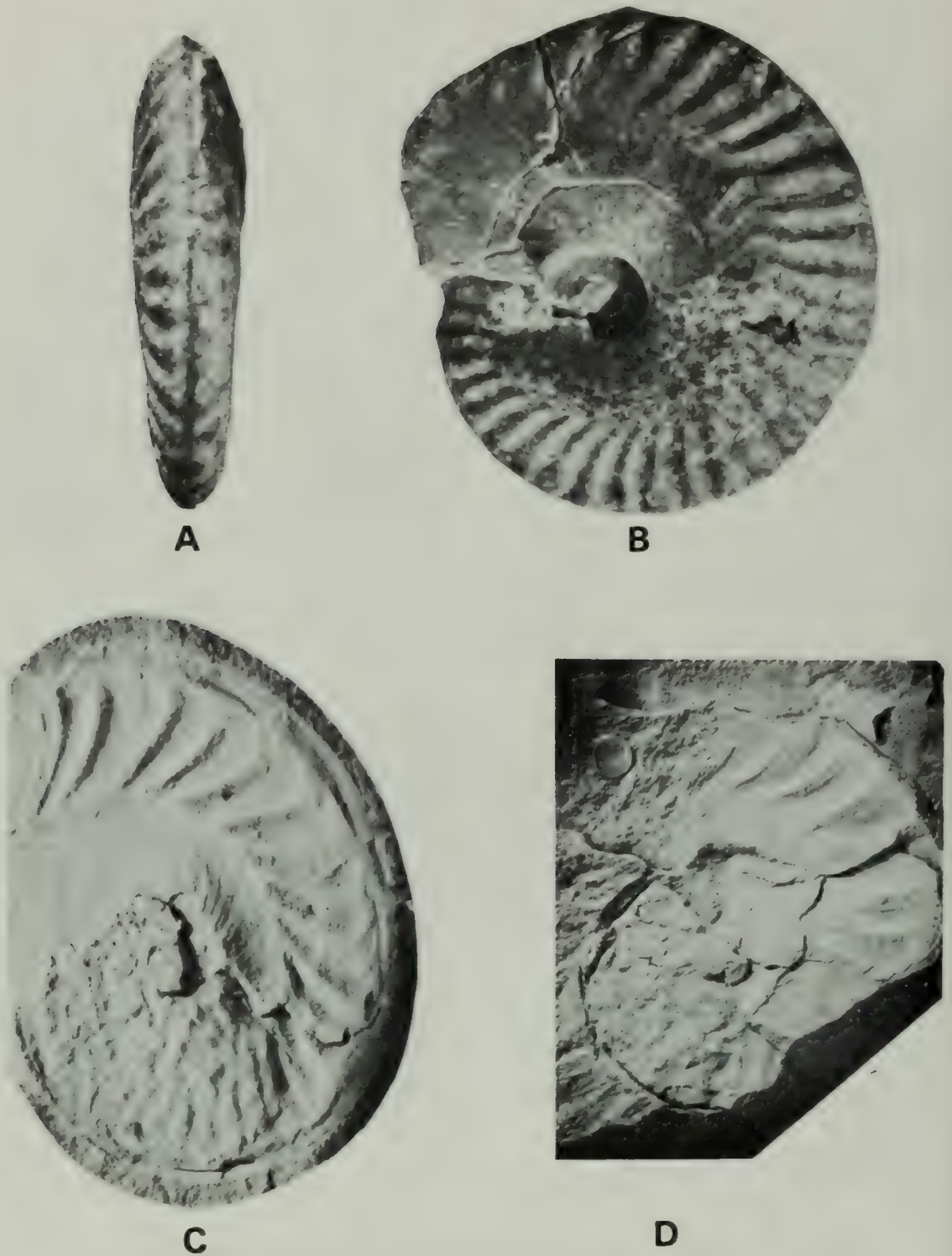


Fig. 5. *Sanmartinoceras* (*Sanmartinoceras*) *paragonicum* Bonarelli, 1921.
A-B. Topotype, after Leanza (1970). C. BMNH C49055. D. BMNH C49057.
C-D. from Alexander Land. $\times 1$.

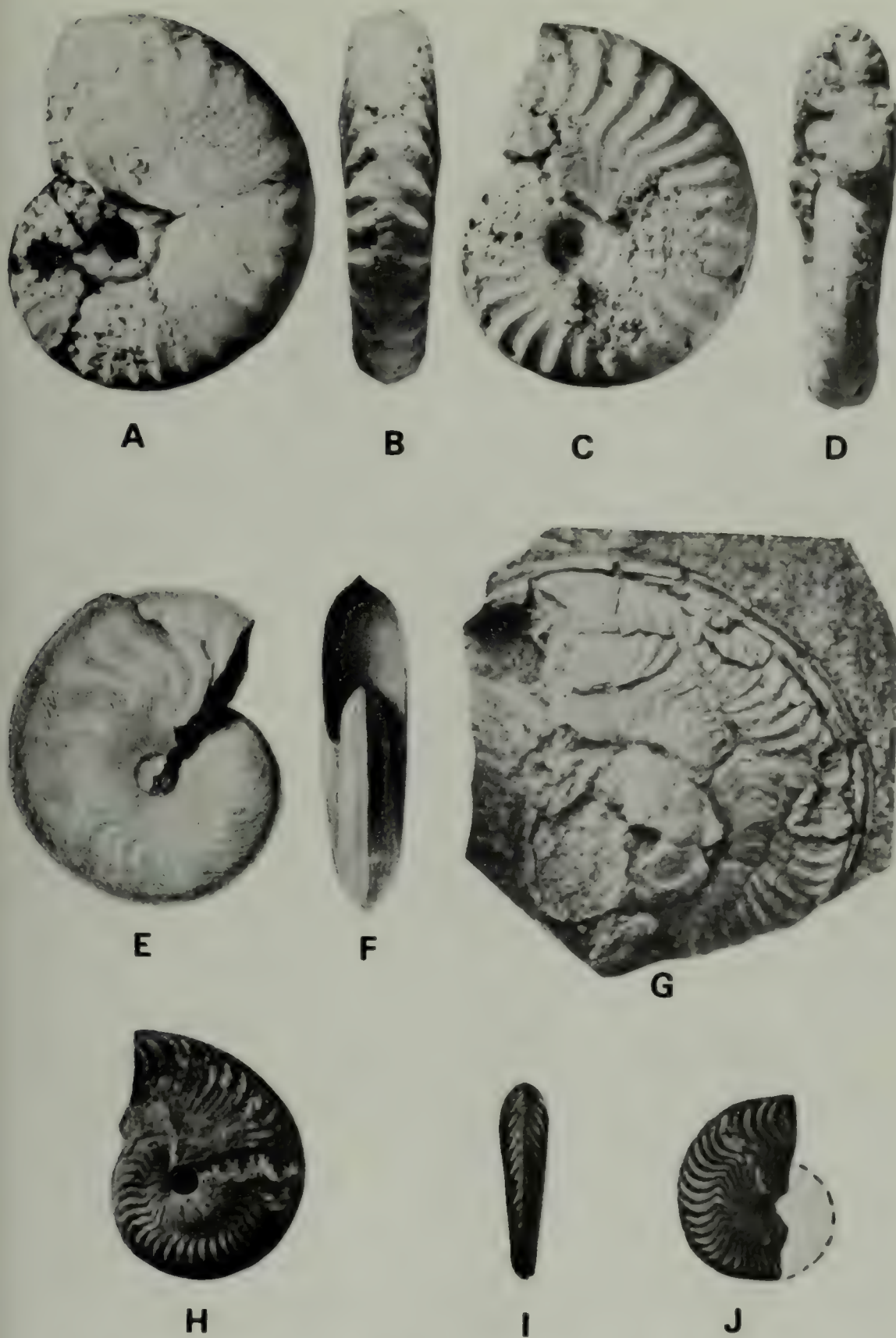


Fig. 6. A. *Sanmartinoceras* (*Sinzovia*) aff. *trautscholdi* (Sinzow), 1870. B-D. *Sanmartinoceras* (*Sinzovia*) *stolleyi* Casey, 1961. BMNH C14365 and 14362, from the Upper Aptian of Bekum, near Hildesheim, Germany. E-F. *Sanmartinoceras* (*Sinzovia*) *trautscholdi* (Sinzow), 1870. Copy of Trautschold (1865). G. *Sanmartinoceras* (*Theganeceras*) *grande* Thomson, 1974. After Thomson (1974). H. *Sanmartinoceras* (*Theganeceras*) *scalatum* von Koenen, 1902. I-J. *Sanmartinoceras* (*Theganeceras*) *falcatum* von Koenen, 1902. H-J after von Koenen (1902). All $\times 1$.

Thomson (Fig. 6G) from the Aptian of Antarctica, have thus far been ascribed to the subgenus, which Casey (1961b: 132) diagnosed as lacking the smooth juvenile stage of *Sanmartinoceras* sensu stricto and having finer, more numerous dense ribs. As is described below, the single Zululand specimen referred to the subgenus suggests that dimorphism may also present taxonomic problems.

The subgenus *Sinzovia* Sazonova, 1958, differs from *Sanmartinoceras* sensu stricto (according to Casey 1961b: 133) in having a very low keel and absence or poor development of a spiral groove. It differs from *Theganeceras* in having a longer juvenile smooth stage and greater tendency to smoothness on the lower flank. The type species is illustrated here as Figure 6E–F, related German species as Figure 6A–D, and the only South African representative, *S. (S.) trautscholdi* (Sinzow), as Figure 7I–K.

Occurrence

Sanmartinoceras and its subgenera range from Upper Barremian to Aptian and are known from Greenland, western Europe, the U.S.S.R., Zululand, Madagascar, Nepal, Australia, Antarctica, Argentina and Papua.

Subgenus *Sanmartinoceras* sensu stricto

Sanmartinoceras (Sanmartinoceras) africanum sp. nov.

Figs 4A–H; 8A–F; 9A–I; 10A–F; 11A–B; 12A–C; 13A–F; 14A–C; 15F–J; 16–17; 19D–E

Sanmartinoceras Kennedy & Klinger 197: 274.

Types

The holotype is SAS H54; paratypes are BMNH C79977–C80001, SAS H54/41a–d, SAS ZO(i), SAS LJE131a, SAS LJE112, SAS H54/17, SAS H54/33, all from the Makatini Formation, Barremian I–II, locality 170, Mlambongwenya Spruit, northern Zululand.

Diagnosis

A large (up to 120 mm diameter phragmocone) species of *Sanmartinoceras* in which the inner ‘haft’ of the ribs is narrow, straight and prorsiradiate and the outer ‘blade’ broad and markedly concave.

Dimensions

			<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>
Holotype, SAS H54			—(—)	20,5(—)	42–5(—)	0,48	—(—)
C79985	27,3(100)	6,6(24)	14,8(54)	0,45	4,1(15)
C79978	120,0(100)	28,8(24)	69,8(58)	0,41	7,3(7)
C79984	115,0(100)	24,0(21)	65,5(57)	0,37	11,3(9,8)



Fig. 7. *Sanmartinoceras (Sanmartinoceras) fontinale* (Hudleston), 1890. Holotype, BMNH C5306, Upper Aptian, Primrose Springs, north of Lake Eyre, south Australia. A-D $\times 1$; E-H $\times 2$. I-K. *Sanmartinoceras (Sinzovia) trautscholdi* (Sinzow, 1870). SAM-PCZ5919. $\times 1$.



Fig. 8. *Sanmartinoceras* (*Sanmartinoceras*) *africanum* sp. nov.
A-C. Holotype SAS 54; D-F paratype BMNH C79989. $\times 1$.

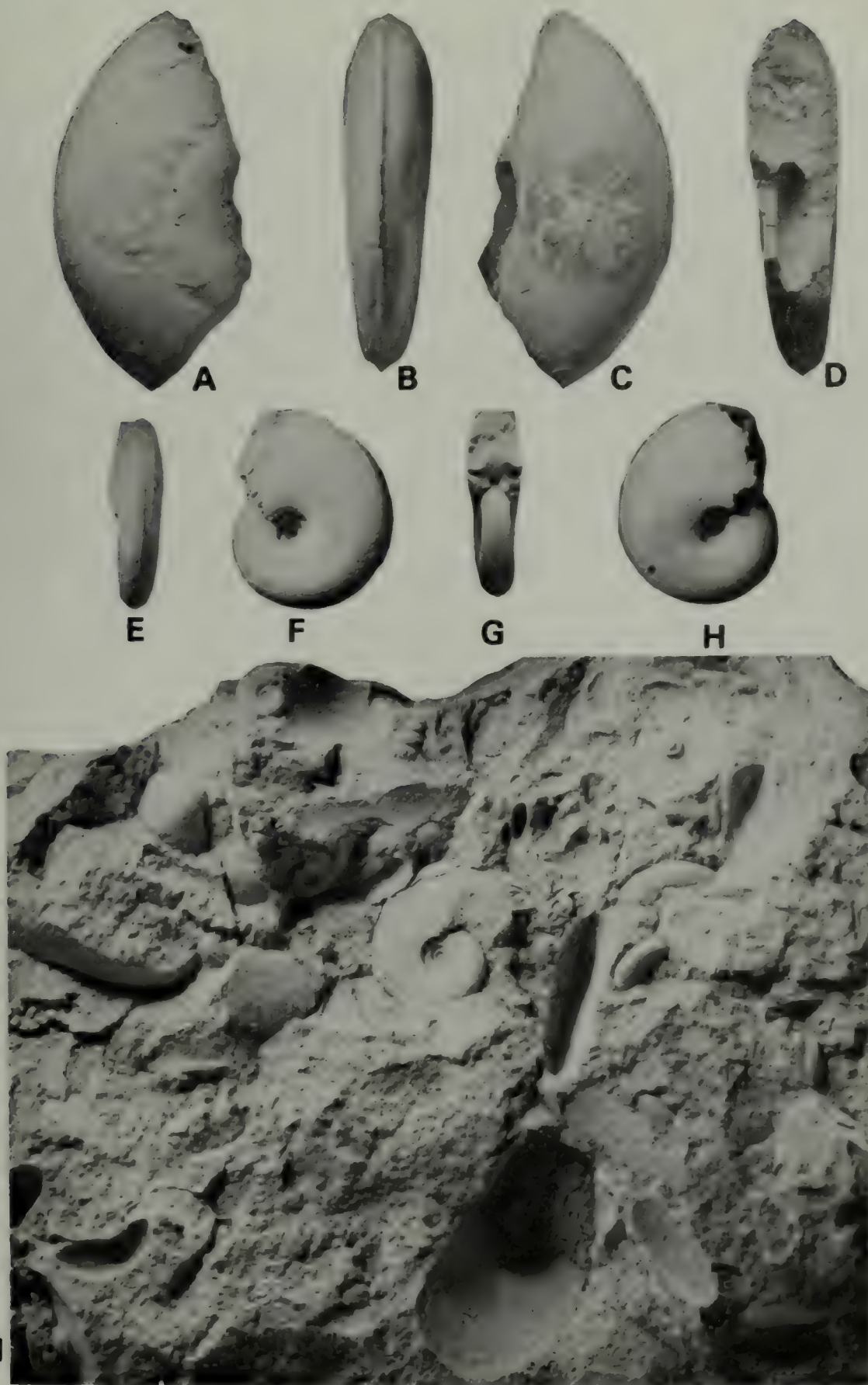


Fig. 9. *Sanmartinoceras* (*Sanmartinoceras*) *africanum* sp. nov., paratypes.
A-D. SAS H54/416. E-H. SAS H54/41a. I. BMNH C79996. All $\times 2$.

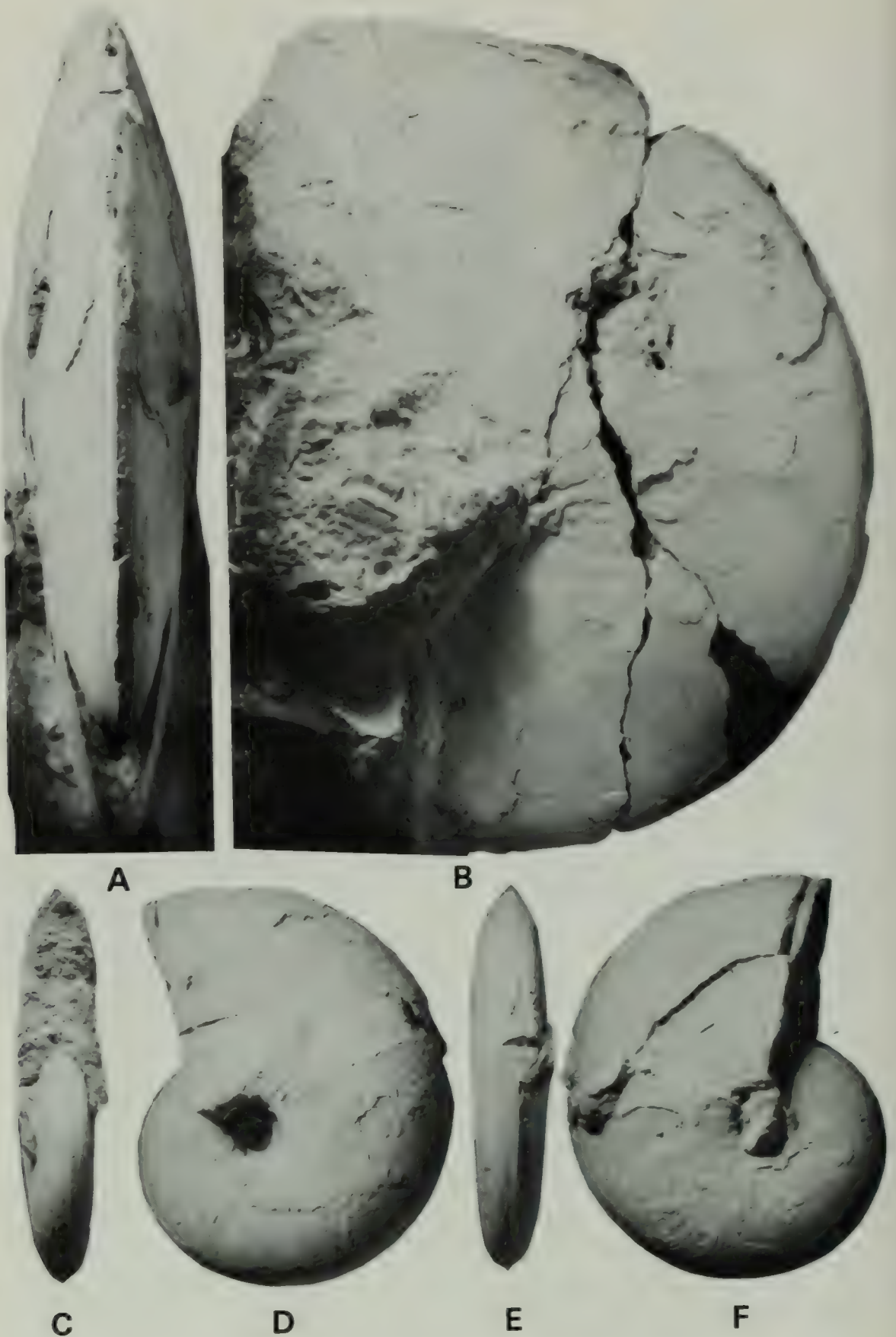


Fig. 10. *Sanmartinoceras* (*Sanmartinoceras*) *africanum* sp. nov., paratypes.
A-B. BMNH C79984. C-F. SAS H54/41c. A-B $\times 1$; C-F $\times 2$.

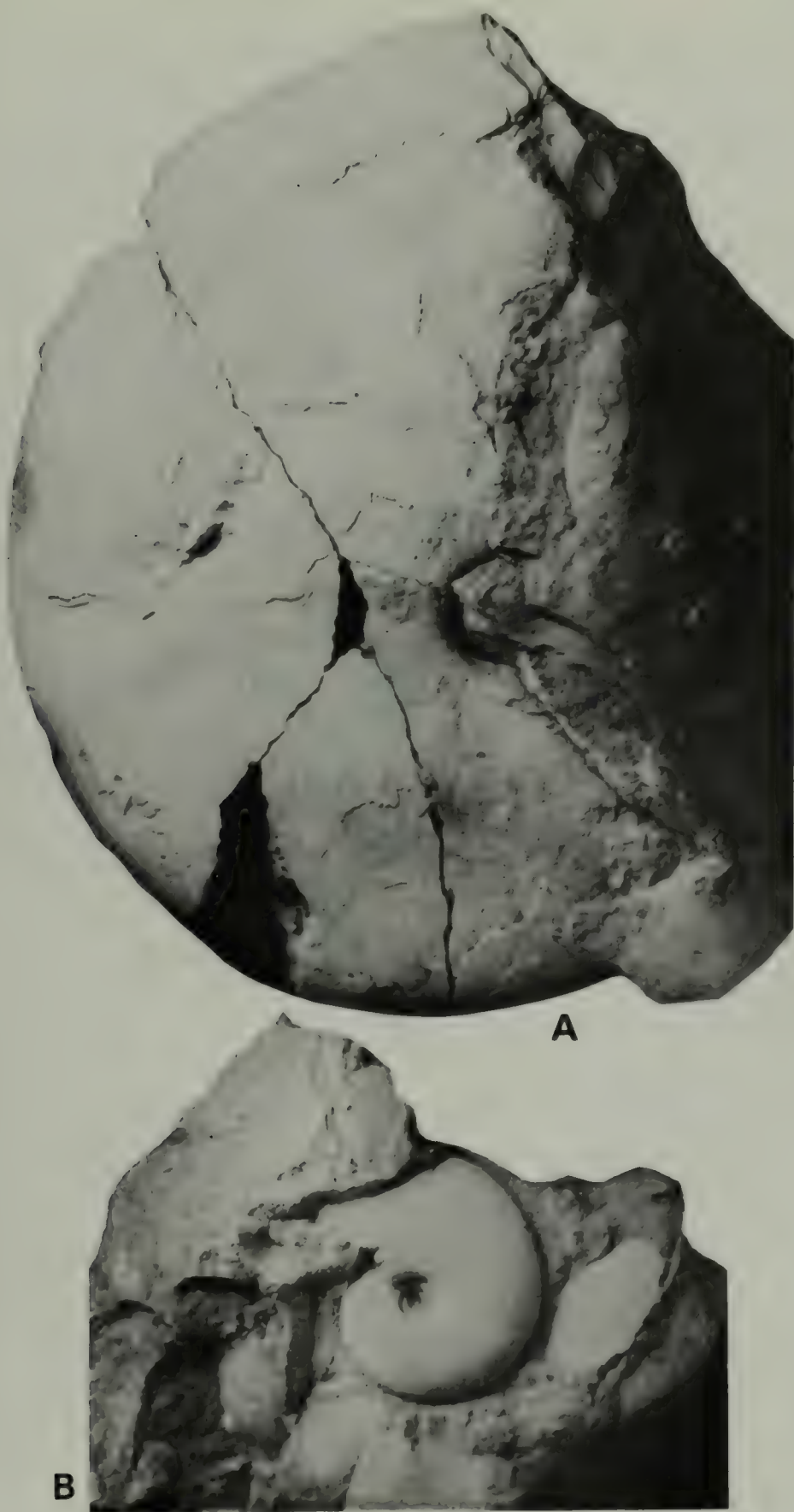


Fig. 11. *Sanmartinoceras* (*Sanmartinoceras*) *africanum* sp. nov., paratypes.
A. BMNH C79984. B. SAS H54/41d. A $\times 1$; B $\times 2$.

Description

The barrel-shaped protoconch is succeeded briefly by rather stout whorls, beyond which, up to a diameter of 0,5–0,8 mm, the shell is moderately involute, slightly compressed, with flattened flanks and a rounded venter. All the available specimens are partially or wholly exfoliated, and any ornament, if present, must have been weak. A few specimens begin to show traces of a ventral ridge, but not a keel at this diameter, although these features may be an artefact of preservation.

From 0,8 mm onwards the shell is an oxycone, the coiling is very involute, with a tiny, crater-like umbilicus. The umbilical wall is flat and subvertical, with an abruptly rounded shoulder. The whorl section varies markedly; stout individuals have a whorl breadth to height ratio of 0,6; in slender individuals the figure is 0,4. Maximum whorl breadth is low on the flanks; the inner flanks are flattened, the outer flanks convergent; a distinct ventrolateral shoulder is developed, and there is a sharp keel which, when well preserved, can be seen to be minutely crenulated (Fig. 9E–H).

Ornament varies greatly. In some individuals (Figs 11B, 13C–D) there are only the finest growth striae. These arise at the umbilical seam, but are very weak. They pass forwards across the inner flank, strengthening as they do so, and sometimes splitting (Fig. 15G–J). They are at their maximum development at mid-flank, where they flex gently backwards, giving rise to a clear concavity which extends across the outer third of the flank (Fig. 13D). Striae decline on the ventrolateral shoulder and project strongly forwards to meet the keel at an acute angle. Individual striae correspond to individual crenulations on the keel. In robust specimens, e.g. BMNH C79983, striae are accompanied by distant, pronounced ribs, which are strongest at mid-flank; there is every intermediate between.

Middle growth stages are also characterized by a wide range of variation (Figs 4E–H, 8A–F). The holotype demonstrates the features of a strongly ornamented individual. It is wholly septate (Fig. 8B) retaining traces of shell. Coiling is very involute, with most of the inner whorls being covered. The tiny umbilicus is deep, with a high, flat, subvertical wall, abruptly rounded shoulder, and faint umbilical carina. The whorl section is compressed (breadth to height ratio is 0,48) with faintly concave inner flanks, a weakly inflated mid-flank region converging to distinct shoulders, clearly demarcated from a high, septate ventral keel. In none of the medium-sized specimens does the keel bear serrations. Ornament consists of fine, rectiradiate striae on the inner part of the flank, effaced at a spiral mid-flank depression. The outer flank bears low, blunt, concave ribs, declining at the ventrolateral shoulder, but projected forwards to meet the keel.

The largest available specimens are up to 120 mm in diameter, and are still wholly septate (Fig. 12A–C). In these, the whorls are quite robust, and ornament consists of striae on the inner flank with blunt, concave ribs on the outer flank. None of the present specimens has the aperture preserved. A few fragments show



Fig. 12. *Sanmartinoceras* (*Sanmartinoceras*) *africanum* sp. nov., paratype BMNH C79978. $\times 1$.

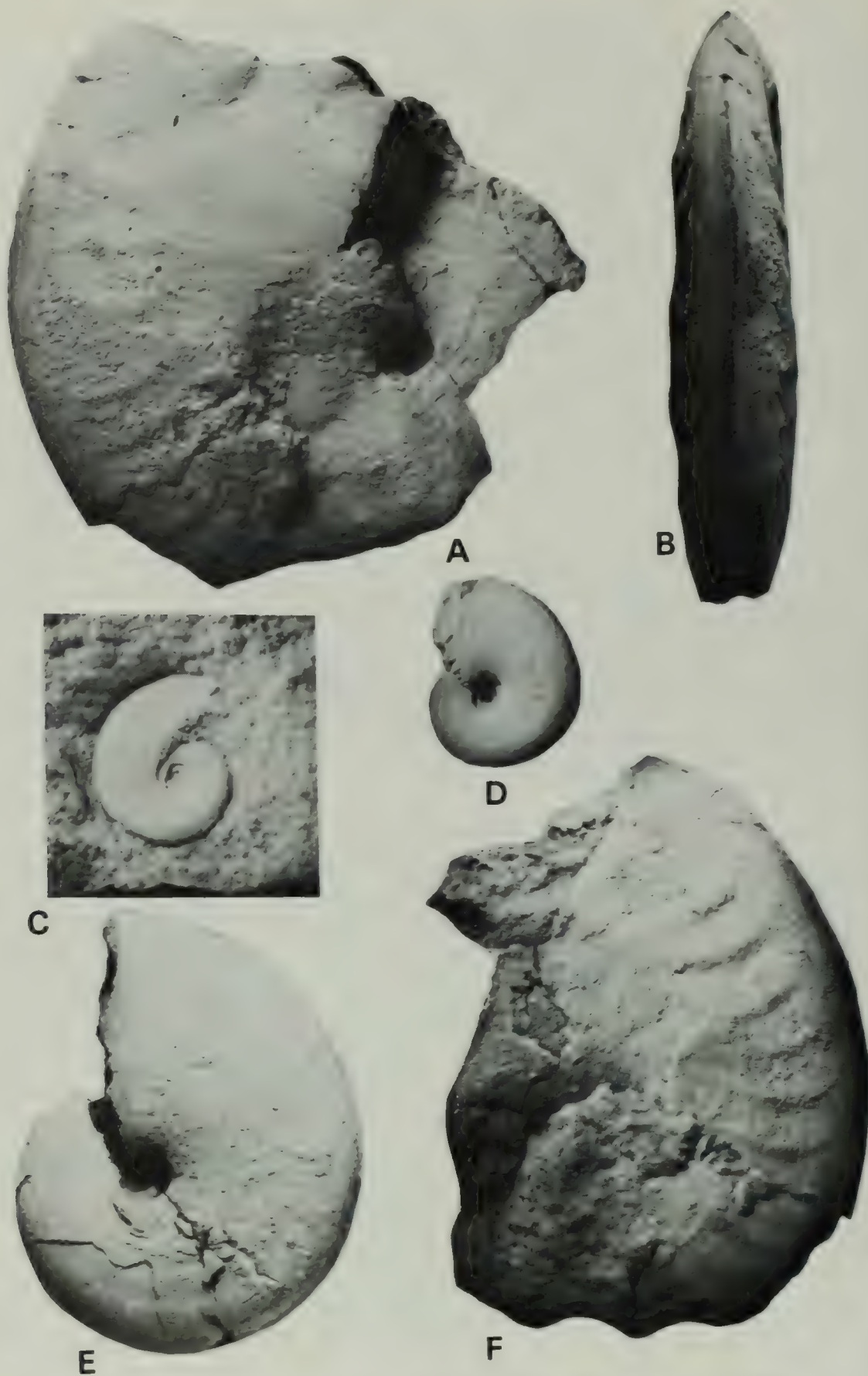


Fig. 13. *Sanmartinoceras* (*Sanmartinoceras*) *africanum* sp. nov., paratypes.
 A-B, F. SAS Zo(i). C. SAS LJE 131a. D. SAS H54/41a. E. BMNH C79979.
 A-D, E-F $\times 1$; C-D $\times 2$.



Fig. 14. A-C. *Sanmartinoceras* (*Sanmartinoceras*) *africanum* sp. nov., paratype SAS LJE 112. D-F. *Borissiakoceras* sp., M. R. Cooper Collection no. 16. A-C $\times 1$; D-F $\times 2$.

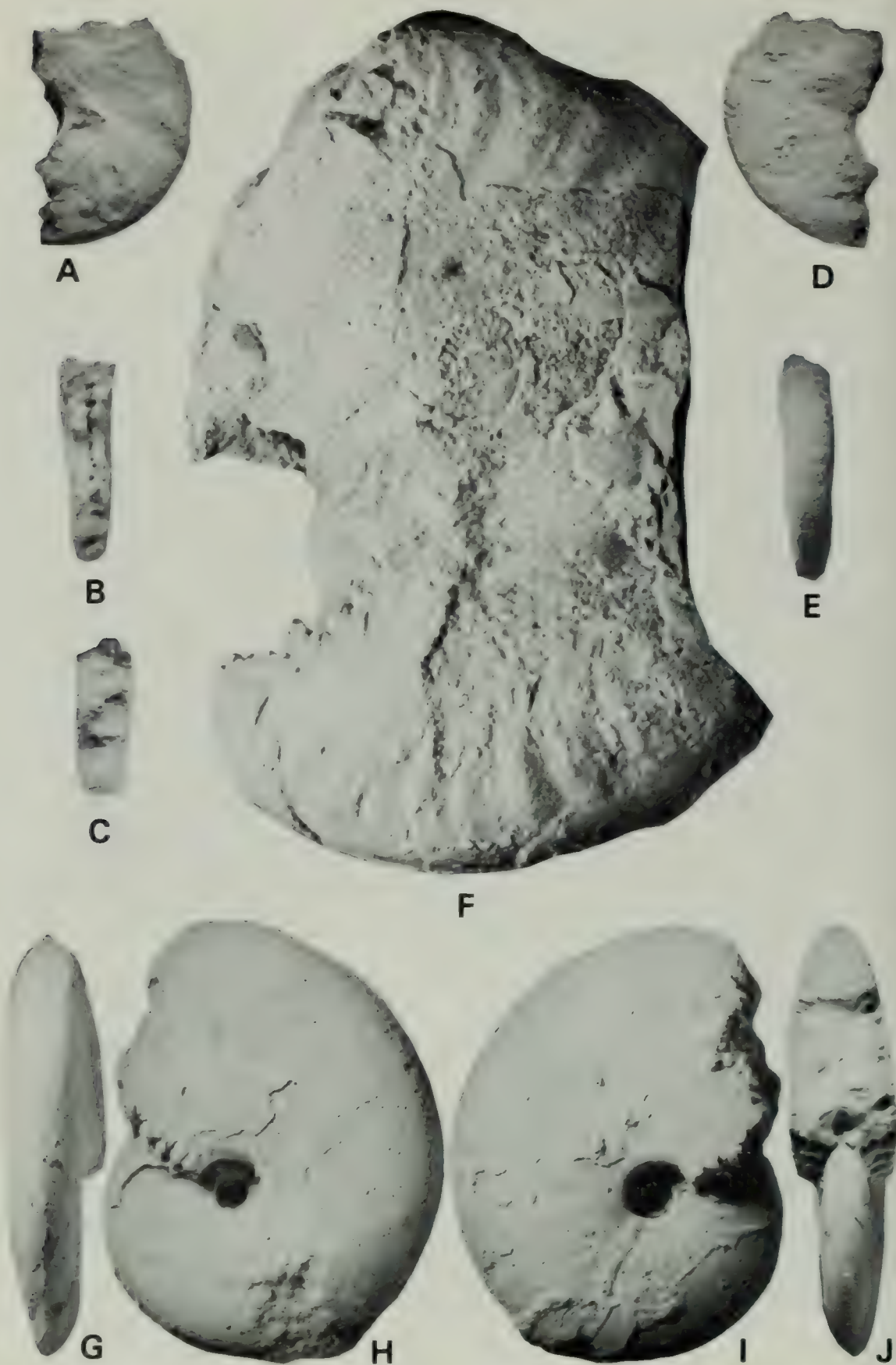


Fig. 15. A-E. *Borissiakoceras* sp., BMNH C80003. F-J. *Sanmartinoceras* (*Sanmartinoceras*) *africanum* sp. nov., paratypes. F is SAS LJE 112; G-J is BMNH C79985.
A-E, G-J $\times 2$; F $\times 1$.

weak to strong strigations (Figs 4B–D, 13E). Where well preserved, this appears to be a feature of the dorsal shell layer, and not of the original external shell surface. That this occurs in some very large specimens suggests the species may have reached diameters close to 200 mm.

The available specimens show the details of suture development to advantage, as shown in Figure 16.

Mature sutures are deeply and intricately subdivided, as shown in Figure 17.

Discussion

The specimens show the ontogeny and range of intraspecific variation far better than in any previously described *Sanmartinoceras* whilst the specimens are the largest known for the genus. It is most unfortunate that none of the specimens retains apertures, but the rather distinct spiral flank depression present in the holotype suggests that it may be a microconch; the largest individuals (Figs 10A–B, 11A, 12A–D) are probably macroconchs.

Thomson (1974: 23) reviewed criteria used to differentiate species of *Sanmartinoceras* as follows:

- (i) strength and form of ribbing,
- (ii) the way in which ribs appear (i.e. abruptly or increasing gradually in strength),
- (iii) the size of the individual at which ribs first appear.

In his discussion, however, he concluded that the form of the falcate ribbing alone was sufficient to separate species. Figure 18 compares the line of ribs and striae in the five described species; on this criterion alone it can be seen that the straight 'haft' and form of 'sickle' of the present species are quite different from the markedly biconcave rib of *S. olenae*, *S. fontinale* and *S. patagonicum*. A straight 'haft' characterizes *S. groenlandicum* (Fig. 18), but here the 'blade' is much more deeply concave with the inner half almost straight. As noted elsewhere, the authors do not regard the presence or absence of a lateral spiral groove as of specific significance, whilst the present specimens vary greatly in strength of ornament and growth stage at which it appears. The other feature which separates *S. africanum* from other species is its great size, but this may be no more than an artefact of preservation.

Occurrence

Upper Barremian of Zululand only.

Subgenus *Theganeceras* Whitehouse, 1927

Theganoceras nodosum sp. nov.

Figs 19A–C, 20

Holotype

SAM-PCZ5708 from the Makatini Formation, Aptian I, locality 170, Mlambongwenya Spruit, northern Zululand.

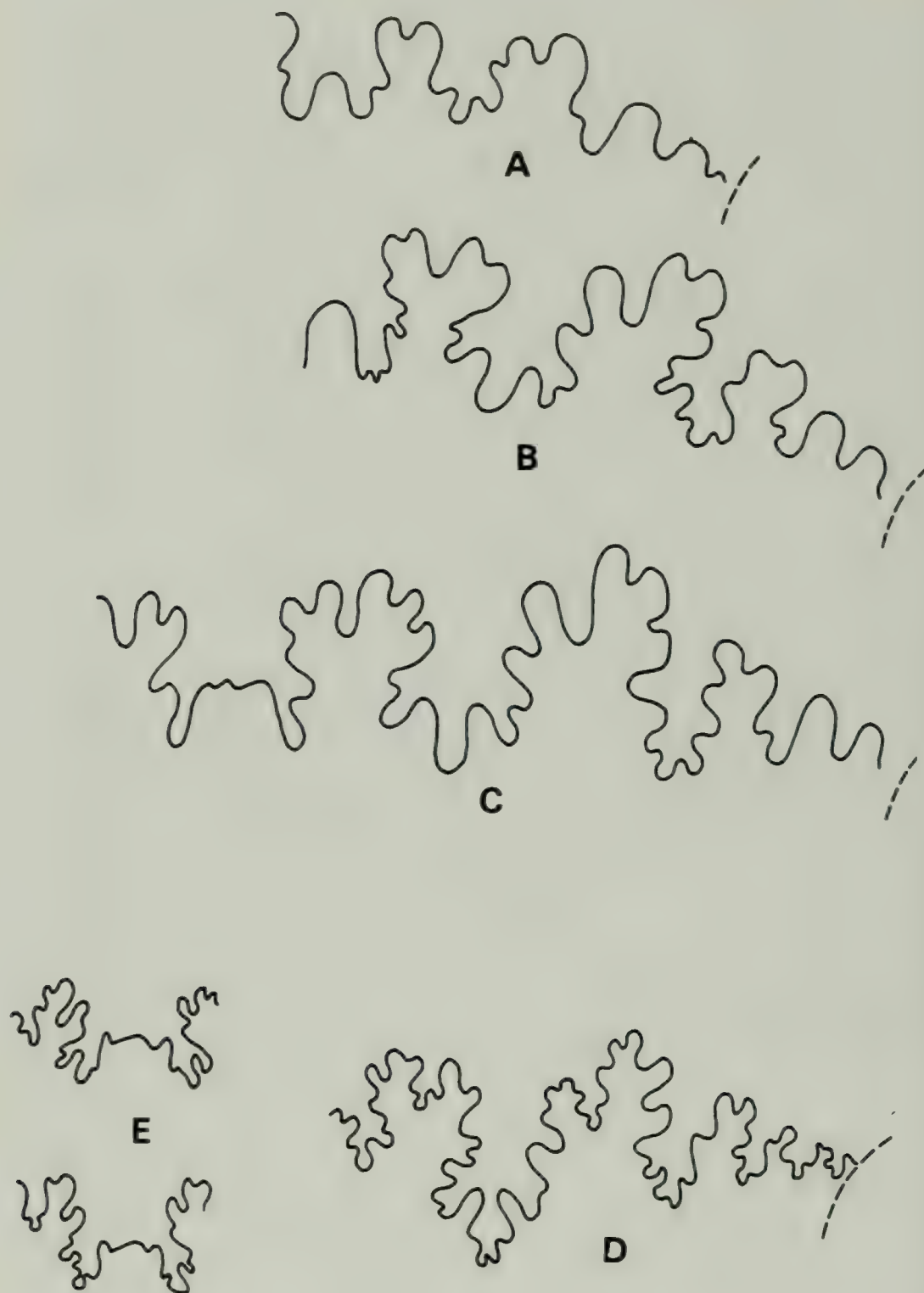


Fig. 16. Suture development in *Sanmartinoceras* (*Sanmartinoceras*) *africanum* sp. nov.
A-C. BMNH C79979. D-E. SAS H54/41A. All $\times 12,5$.

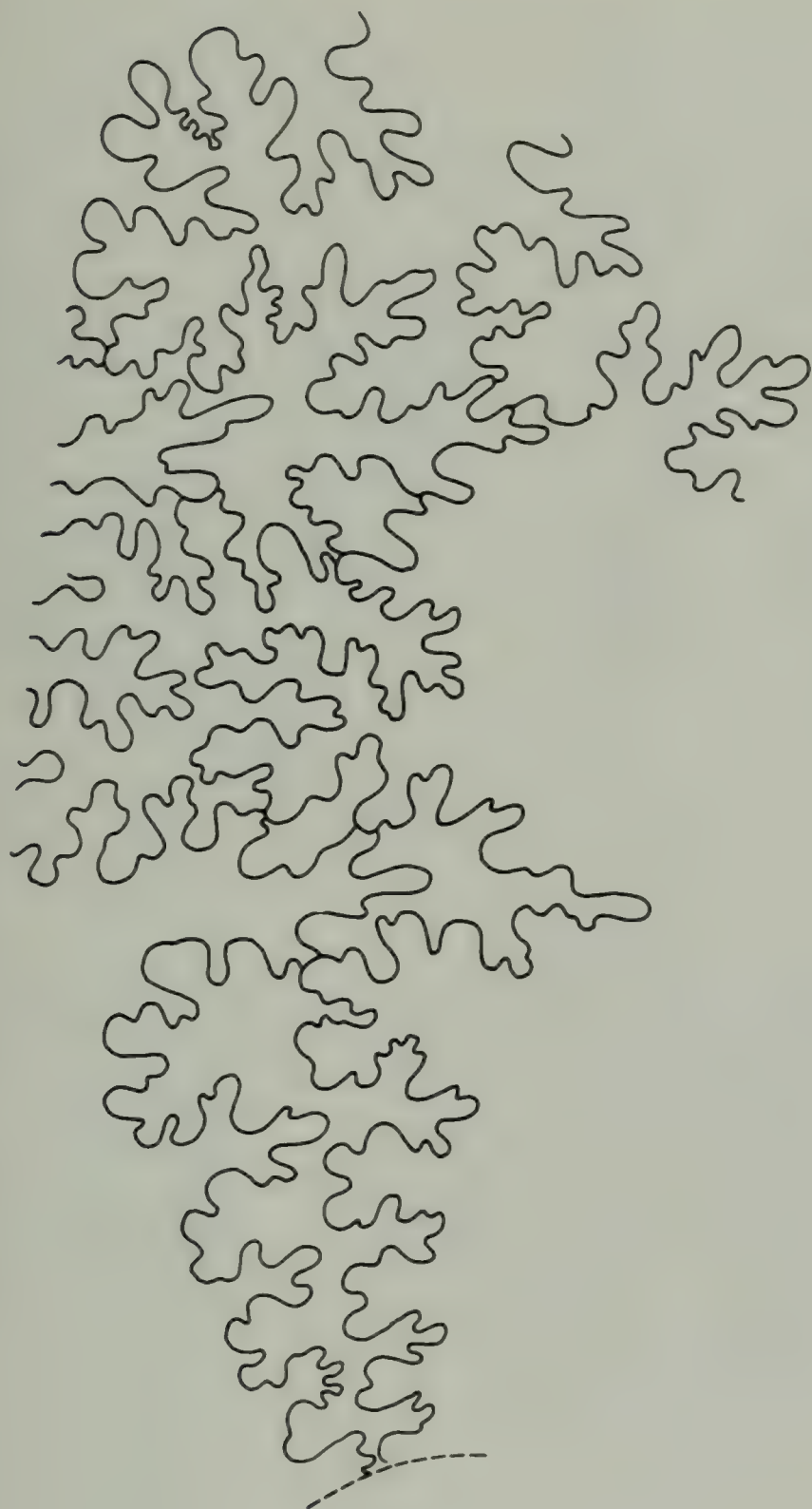


Fig. 17. Mature sutures of *Sanmartinoceras* (*Sanmartinoceras*) *africanum* sp. nov. SAS H54/41c. $\times 12,5$.

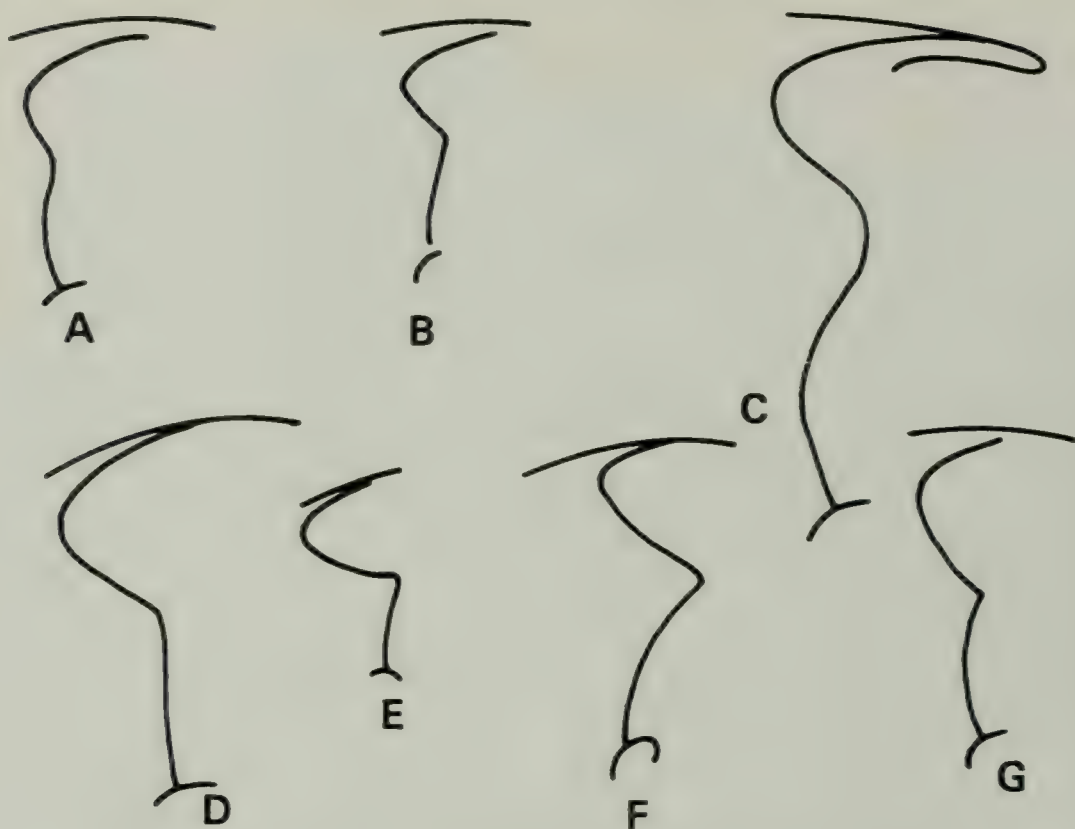


Fig. 18. Rib patterns in *Sanmartinoceras* (*Sanmartinoceras*) compared.
 A. *S. (S.) olenae*. B-C. *S. (S.) fontinale*. D. *S. (S.) africanum*. E. *S. (S.) groenlandicum*.
 F-G. *S. (S.) patagonicum*.

Diagnosis

A large species of *Theganoceras* with broad, flat, falcoid ribs on the inner whorls which bear umbilical bullae and incipient ventral clavi. Outer whorls ornamented by bullae, flexuous growth lines, folds and constrictions.

Description

The unique holotype of this species comprises a crushed body chamber and a nucleus. Growth of calcite between shell and sedimentary infilling has produced an unduly thick 'shell' of partly diagenetic origin.

The inner whorl, at a diameter of approximately 38 mm, bears fourteen to sixteen closely spaced, low, broad, sickle-shaped ribs which are straight and prorsiradiate on the inner flank, flexing backwards at mid-flank and becoming markedly concave on the outer flank. The ribs are strong and well developed down to the umbilicus where a distinct bulla is present, whilst on the ventro-lateral shoulder they strengthen into an incipient clavus. The ribs themselves and interspaces between bear dense striae, sometimes strengthened into riblets, giving some ribs a bunched, fasciculate appearance. The venter is fastigate, and bears strongly projected striae.

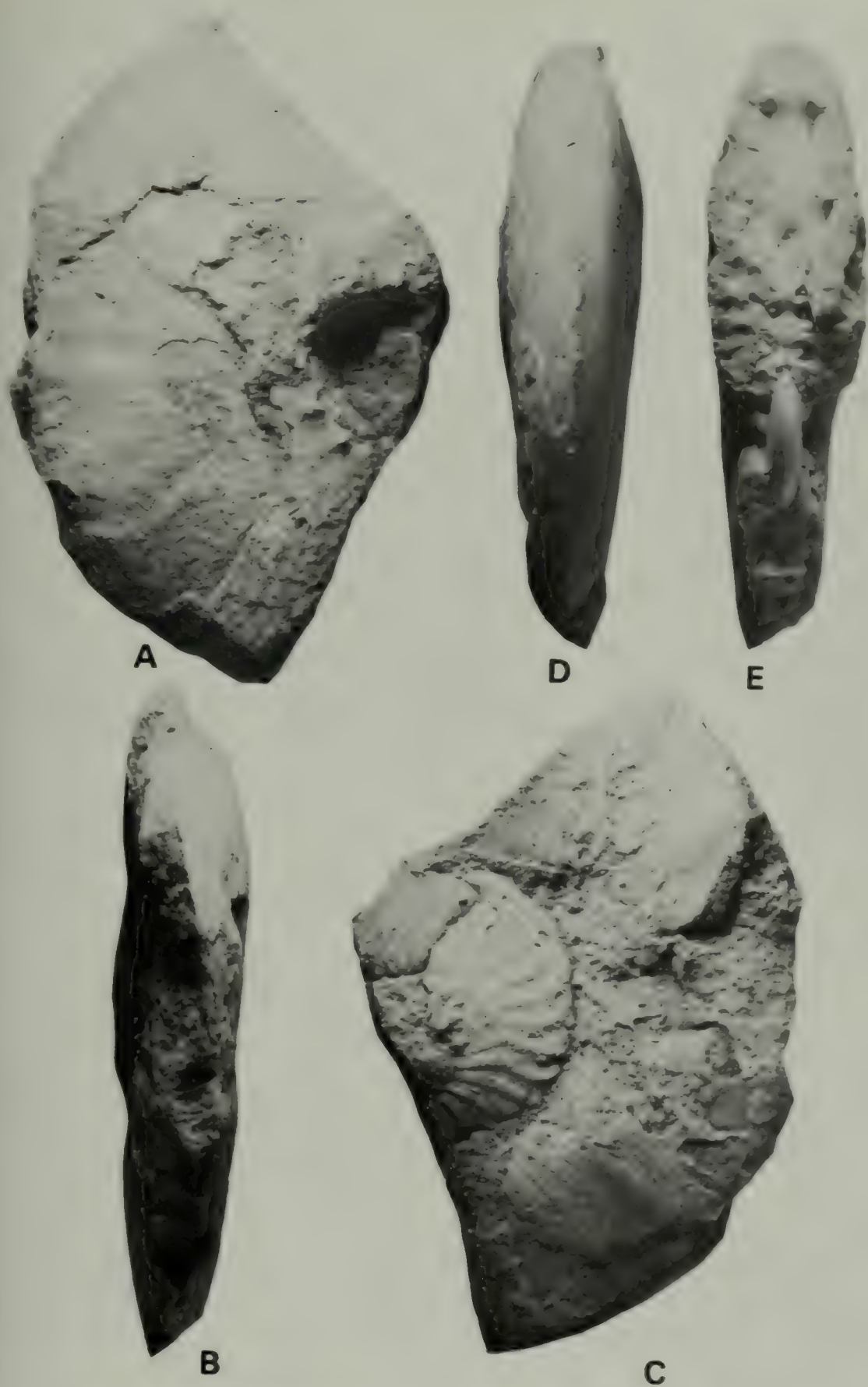


Fig. 19. A-C. *Sanmartinoceras* (*Theganeceras*) *nodosum* sp. nov., holotype, SAM-PCZ5708. $\times 1$.
 D-E. *S.* (*Sanmartinoceras*) *africanum* sp. nov., paratype, BMNH specimen. $\times 1$.

The outer body whorl shows coiling to have been involute with a moderately large, deep, crater-like umbilicus with a flat, outwards-sloping wall. The whorl section is compressed, lanceolate, so that the overall shell form was an oxycone. The whorl breadth to height ratio is estimated as approximately 0.38, the greatest breadth being close to the angular umbilical shoulder. The preserved fragment bears seven small, sharp, comma-shaped bullae at the shoulder. These give rise to bundles of fine, dense, flexuous striae which, being crowded close to the umbilicus, appear as ribs, which fade out at a short distance from the bulla. The striae flex forwards to mid-flank, then backwards, to form the very shallow blade of a sickle. They are strongly projected across the ventro-lateral shoulder. Paralleling these striae are irregular, low folds and constrictions.

The imperfectly exposed suture is illustrated in Figure 20.

Discussion

The presence of well-developed ribs which extend to the umbilical shoulder indicates this specimen to be a *Theganeceras*. It differs from all previously described species in having broader, less markedly flexed ribs when young, as well as possessing umbilical bullae, which feature is unique for the subgenus. Only *S. (Theganeceras) grande* Thomson (1974, pl. 4 (fig. 9)) approaches this specimen in size; the unique holotype of that species is quite distinct, however, lacking bullae and having strongly flexed ribs and striae (Fig. 6G).

Equally, no *S. (Sinzovia)* bears bullae, and the closest species, *S. (S.) stolleyi* Casey (Fig. 6A–D), has ribs which efface on the inner flank. The presence of bullae also distinguishes our specimen from described *S. (Sanmartinoceras)* at comparable dimensions.

Occurrence

Lower Aptian I of northern Zululand only.

Subgenus *Sinzovia* Sazonova, 1958

Sanmartinoceras (Sinzovia) trautscholdi (Sinzow)

Figs 4I–K, 6E–F

Ammonites bicurvatus Trautschold (*non* Michelin), 1865: 22, pl. 3 (figs 17a–c).

Oppellia Trautscholdi Sinzow, 1870: 118, pl. A (figs 1, 1a–b only).

Sinzovia trautscholdi (Sinzow): Sazonova, 1958: 128, pl. 6 (fig. 2), pl. 8 (figs 1, 1a, 3–7), pl. 10 (figs 4–5) (with synonymy). Druschchitz & Kudryavtseva, 1960: pl. 42 (figs 7a–b).

Collignon 1962: 31, pl. 229 (fig. 974).

? *Sanmartinoceras (Sinzovia)* sp. cf. *trautscholdi* (Sinzow): Casey 1961b: 136, pl. 26 (fig. 7).

Holotype

Trautschold's original of his plate 3 (fig. 17a–c), from the Lower Aptian of Simbirsk (now Polivna) in the Stalingrad area of Russia, on which Sinzow (1870: 118) based his species. The original figures are reproduced here as Figure 6E–F.

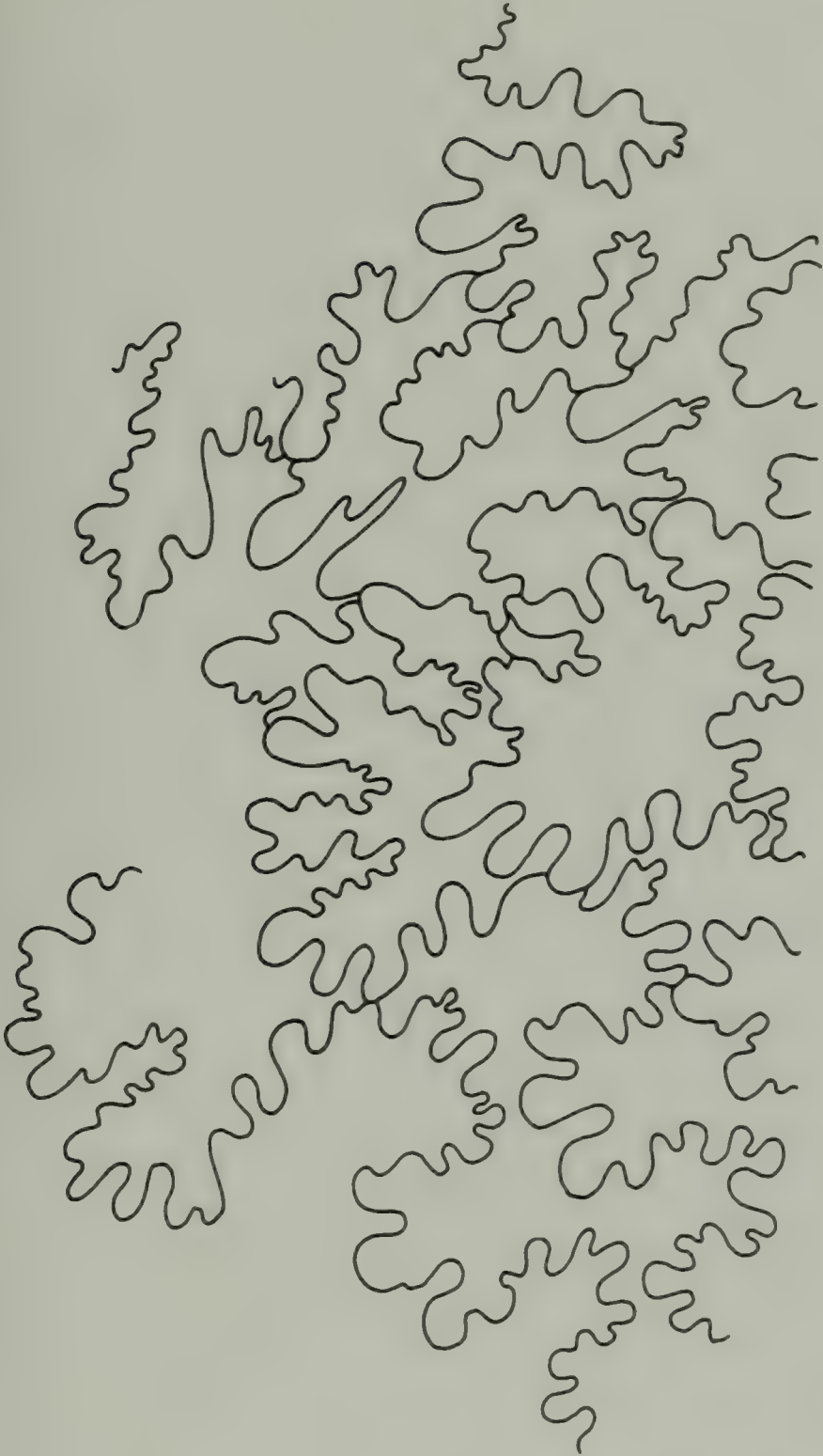


Fig. 20. *Sanmartinoceras* (*Theganeceras*) *nodosum* sp. nov., partial suture of the holotype, SAM-PCZ5708. $\times 12,5$.

Material

SAM-PCZ5919 from the Makatini Formation, Aptian IV at locality 152, Mkuze Game Reserve, northern Zululand.

Description

The specimen is a beautifully preserved disc of which the last half of a whorl is body chamber. It retains extensive areas of replaced shell, in consequence of which the sutures are not fully decipherable. The dimensions are as follows:

<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>
43,0	10,0(23,3)	22,0(51,2)	0,45	9,0(20,9)

Coiling is very involute, oxycone, with two-thirds of the previous whorl being covered. The umbilicus is small and shallow (20% of diameter), with a flat, subvertical wall. The umbilical shoulder is sharp and angular. The whorl section is very compressed, with a breadth to height ratio of 0,45. The inner flank is flattened to concave, with gently rounded, convergent outer flanks, converging to an acute, delicately keeled venter.

The inner, concave part of the flank is virtually smooth where shell is present, due to weathering. On the mould, however, there are delicate, concave, prorsiradiate, bunched striae which sweep forwards to a distinct spiral ridge at mid-flank and a parallel groove external to this. On the ridge and groove, the striae flex backwards in a marked convex projection. On the outer flank, they flex backwards to form a 'blade' corresponding to the bunches of 'handles' to what is an overall sickle-like ornament. The blades are strong, concave, blunt ribs, strong over most of the last whorl, although effacing on the venter, which is smooth on either side of a narrow, sharp ventral keel.

The sutures cannot be seen.

Discussion

On the basis of weakness of inner flank ornament, and strength and style of ribs on the outer flank, the authors would refer their single specimen to Sinzow's species. It is particularly close to the specimen from Ulyanovsk, Russia, illustrated by Casey (1961*b*, text-fig. 143 (1a-b)).

Sinzovia stolleyi Casey (1961*b*, text-fig. 143(g)) is more distantly and narrowly ribbed, as can be seen from Figure 6A-D herein.

Sinzovia aptianum (Sarasin) (1893: 155, pls 4-6 (fig. 12a-c); Casey 1961*b*: 134, pl. 26 (fig. 6a-b)) has blunter, fewer ribs on the outer flank.

Sanmartinoceras? (*Sinzovia?*) sp. nov. of Casey (1961*b*: 136, text-fig. 43(f)) is a Lower Albian species of uncertain affinity.

Occurrence

Lower Aptian of the U.S.S.R. and southern England; Upper Aptian of Madagascar and Zululand.

Family *Binneyitidae* Reeside, 1927

The *Binneyitidae* are a family of micromorphs, characteristically platycone, with much reduced sutures. Two genera, *Borissiakoceras* Arkhangelsky, 1916, and *Binneyites* Reeside, 1927, were referred to the family by Wright (1957) who suggested derivation from the *Acanthocerataceae*, but subsequent work has revealed the presence of passage forms linking the family to the *Aconeceratidae* via *Falciferella* Casey, 1954. This Middle to Upper Albian genus has a vestigial keel when young and can be linked to the platycone but still feebly carinate Aptian aconeceratids *Doridiscus* Casey, 1961, and *Nothodiscus* Casey, 1962 (in Collignon 1962). The evolutionary origins of the family thus involved a change from oxycone to platycone with corresponding loss of keel, and sutural simplification.

Genus *Borissiakoceras* Arkhangelsky, 1916*Type species*

Borissiakoceras mirabile Arkhangelsky, 1916.

Diagnosis

Small, compressed, moderately involute to moderately evolute platycones. Flanks typically smooth, sometimes bearing narrow, falcoid ribs. A few species bear ventrolateral tubercles. Suture simple with narrow, bifid lobes and broader, bifid or trifid saddles.

Discussion

Borissiakoceras is a distinctive genus, differing obviously from the later (Coniacian) *Binneyites* Reeside, 1927, which has stronger lateral and ventrolateral ornament, sharp ventrolateral shoulders and more auxiliary elements in the suture. *Johnsonites* Cobban, 1961, has a simpler suture and a flat or concave venter.

Borissiakoceras is clearly descended from *Falciferella*, species of which extend to the Upper Albian. It is the only binneyitid in which dimorphism has been demonstrated (Kennedy & Cobban 1976: pl. 1 (figs 3–4)); males have stronger, more markedly biconcave growth striae and ribs, reflecting a similar aperture, with a short rostrum.

Occurrence

Borissiakoceras is best known from North America, ranging from Texas (Stephenson 1952, 1955) to Kansas and Colorado (Morrow 1935). Other United States occurrences are summarized by Cobban (1961). It also occurs in British Columbia (Warren & Stelck 1958) and Alaska (Cobban & Gryc 1961). In these regions it ranges from Middle Cenomanian to Lower Turonian. The type species comes from Turkestan and is probably of late Cenomanian age;

Bodylevsky & Shulinga (1958) record the genus from the Turonian–Coniacian of the northern U.S.S.R., and Kennedy & Juignet (1973) record it from the Middle Cenomanian of Normandy, whilst the present authors have seen a fragment from the Lower Cenomanian of Sarthe (Sorbonne collections). Wright (1963) records a doubtful species from the Middle Cenomanian of northern Australia, and the Engonoceratidae gen. et sp. nov. of Henderson (1973: 106, pl. 14 (fig. 8)) belongs here, as do the Middle Cenomanian specimens from Zululand described below.

Borissiakoceras sp.

Figs 14D–F, 15A–E

Material

Two specimens, BMNH C80003, and no. 16 in M. R. Cooper's collection, University of Natal, Durban, both from the Middle Cenomanian (Cenomanian III) Locality 62, the Skoenberg, Zululand.

Description

The specimens comprise a small phragmocone and a body chamber with a maximum whorl height of 7.4 mm. Coiling is involute with a small, shallow umbilicus comprising approximately 20 per cent of the diameter. The overall form is platycone, the whorl breadth to height ratio being approximately 0.5, with a low umbilical wall, flattened inner, and slightly convergent outer flanks, abruptly and narrowly rounded ventrolateral shoulder, and somewhat flattened venter. Both specimens are corroded, so that no trace of any original ornament remains. The suture is poorly exposed, but much simplified, with such elements as are visible resembling those of *B. mirabile*.

Discussion

Overall shell form and suture indicate these specimens to be *Borissiakoceras*, the first representatives of the genus, and indeed the Binneyitidae, to be described from Africa. Because of poor preservation it is not possible to identify them fully. They most closely resemble feebly ornamented species such as *B. mirabile* (see Kennedy & Juignet 1973) and *B. orbiculatum* (see Cobban, 1961: 750, pl. 88 (figs 15–41), text-figs 5a–f).

Occurrence

Middle Cenomanian of Zululand.

ANNOTATED LIST OF SPECIES REFERRED TO THE ACONECERATIDAE AND BINNEYITIDAE

Family Aconeceratidae Spath, 1923

Genus *Protacneceras* Casey, 1954

Type species: *Oppelia patagoniensis* Favre, 1908, by original designation.

Protacneceras patagoniense (Favre), 1908: 634, pl. 34 (fig. 7), pl. 37 (figs 3–5), text-fig. 6. Lower Hauterivian of Patagonia.

Protacneceras spp. nov. Casey, 1954: 270, pl. 7 (fig. 7), text-fig. 2. Upper Hauterivian, England.

Genus *Aconeceras* Hyatt, 1903

(= *Adolphia* Stolley, 1907; *Adolphites* Hennig, 1932)

Type species: *Ammonites nissus* d'Orbigny, 1841, by monotypy.

Aconeceras nissus (d'Orbigny), 1841: 184, pl. 55 (figs 7–9). Casey 1961*b*: 128. Upper Aptian of western Europe, notably Gargasian clays of the Vocontian Trough. Also recorded from Madagascar and elsewhere, although many records are dubious.

Aconeceras haugi (Sarasin), 1893: 156, pls 4–6, text-fig. 11a–c. Lower Aptian of western Europe, Nepal (Bordet *et al.* 1971), and Madagascar (Collignon 1962) where it is said to be of Upper Aptian age.

Aconeceras neonisoides Casey, 1961*b*: 129, pl. 26 (figs 1, 9–10), text-fig. 41d–e. Lower Albian of southern England and north Africa (Sornay 1955; Dubourdieu 1956).

Aconeceras australonisoides Brunnschweiler, 1959: 11, pl. 1 (fig. 1a–b). Aptian of western Australia.

Aconeceras whitehousei Brunnschweiler, 1959: 12, pl. 1 (fig. 2a–b). Aptian of western Australia.

Aconeceras walshense (Etheridge), 1892: 493, pl. 42 (figs 10–11). Whitehouse 1926: 203, pl. 34 (fig. 1), pl. 37 (fig. 3); 1927*a*: 114, pl. 16 (figs 2–3), text-figs 1, 6–7. Aptian of Queensland.

Aconeceras nisoides (Sarasin), 1893: 155, pls 4–6 (fig. 10a–c), text-figs 3, 5. Lower Aptian of western Europe.

Aconeceras luppovie (Sazonova), 1958: 130, pl. 8 (fig. 2). Aptian of the U.S.S.R.

Aconeceras saratoviensis (Sazonova), 1958: 130 (= *Oppelia trautscholdi* Sinzow, 1898, pl. A (figs 4–5 only)). Lower Aptian of the U.S.S.R.

Genus *Sanmartinoceras* Bonarelli, 1921

Type species: *Sanmartinoceras patagonicum* Bonarelli, 1921, by monotypy.

Sanmartinoceras (*Sanmartinoceras*) *patagonicum* Bonarelli, 1921, in Bonarelli & Nagera 1921: 27, pl. 5 (figs 3–6). See also Howarth 1958: 5, pl. 1 (figs 6–10); Leanza 1970: 215, fig. 14; Thomson 1974: 24, pl. 4b–f, text-fig. 7a. Aptian of Argentina and Antarctica. (See Fig. 6A–D herein.)

Sanmartinoceras (*Sanmartinoceras*) *groenlandium* Rosenkrantz, 1934, in Bøgvad & Rosenkrantz 1934: 20, pl. 4 (fig. 3), pl. 5 (figs 1–5). Aptian of east Greenland. (See Fig. 1A–C herein.)

Sanmartinoceras (*Sanmartinoceras*) *olenae* (Tenison-Woods), 1883: 150, pl. 7 (fig. 8), pl. 8 (fig. 1). Whitehouse 1926: 205, pl. 41 (fig. 3); 1927*a*: 117, pl. 17 (fig. 6), text-figs 3, 4, 9. Aptian of Australia. (See Fig. 3A–C herein.)

Sanmartinoceras (*Sanmartinoceras*) *fontinale* (Hudleston), 1890: 241, pl. 9 (fig. 1). Whitehouse, 1927*a*: 116, pl. 17 (figs 2–5). Aptian of Australia. (See Figs 3D–G, 7A–H herein.)

Sanmartinoceras (*Sanmartinoceras*) *africanum* Kennedy & Klinger, 1978 sp. nov. (See p. 96.) Upper Barremian of Zululand.

Subgenus *Sinzovia* Sazonova, 1958

Type species: *Ammonites trautscholdi* Sinzow, 1870 (= *Ammonites bicurvatus* Trautschold, 1865 *non* Michelin, 1838) by original designation.

Sanmartinoceras (*Sinzovia*) *trautscholdi* (Sinzow), 1870: 118–119. See also *Ammonites bicurvatus* Trautschold, 1865: 22, pl. 3 (fig. 17a–c) (*non* Michelin); Casey, 1961*b*: text-fig. 135a–c. Lower Aptian of the U.S.S.R. and southern England; Upper? Aptian of Madagascar; Upper Aptian of Zululand.

- Samartinoceras* (*Sinzovia*) *aptianum* (Sarasin), 1893: 155, pls 4–6, fig. 12a–c. Casey 1961b: 134, pl. 26 (fig. 6a–b), text-fig. 43d–e. Aptian of France, southern England and elsewhere in Europe; Nepal (Bordet *et al.* 1971). (See Fig. 6E–F herein.)
- Sanmartinoceras* (*Sinzovia*) *stolleyi* Casey, 1961b: 133, 136; text-fig. 135g–h. Upper Aptian of Germany. (See Fig. 6A–D herein.)
- Sanmartinoceras*? (*Sinzovia*?) sp. nov. Casey, 1961b: 136, text-fig. 43f. Aptian of England.
- von *Sinzovia luppovii* Sazonova, 1958: 130, pl. 8 (fig. 2) = *S. luppovi* Casey, 1961b: 130. Lower Aptian of the U.S.S.R. An *Aconeceras* according to Casey (1961b: 133).
- ?non *Sinzovia saratoviensis* Sazonova, 1958 (= *Oppelia trautscholdi* Sinzow, 1898, pl. A (figs 4–5a only). Lower Aptian of the U.S.S.R. Also an *Aconeceras* according to Casey (1961b: 133).

Subgenus *Theganeceras* Whitehouse, 1926

- Type species: *Oppelia scalata* von Koenen, 1902, by original designation.
- Sanmartinoceras* (*Theganeceras*) *grande* Thomson, 1974: 25, pl. 4g. Lower Aptian of Alexander Island. (See Fig. 6G herein.)
- Sanmartinoceras* (*Theganeceras*) *scalatum* (von Koenen), 1902: 54, pl. 45 (fig. 6). Lower Aptian of north Germany. (See Fig. 6H herein.)
- Sanmartinoceras* (*Theganeceras*) *falcatum* (von Koenen), 1902: 48, pl. 45 (figs 7–8). See also Casey 1961b: 132, pl. 26 (fig. 2). Lower Aptian of north Germany and England. (See fig. 6I–J.)
- Sanmartinoceras* (*Theganeceras*) (?) sp. Thomson, 1974: 26, pl. 4k. Lower Aptian of Alexander Island.
- Sanmartinoceras* (*Theganeceras*) *nodosum* Kennedy & Klinger sp. nov. (See p. 107.) Lower Aptian of Zululand.

Genus *Gyaloceras* Whitehouse, 1927

- Type species: *Gyaloceras smithi* Whitehouse, 1927 by original designation.
- Gyaloceras smithi* Whitehouse, 1927a: 115, pl. 17 (fig. 1), text-fig. 8. Aptian of Australia. (See Fig. 2A.)
- Gyaloceras ibo* Reyment, 1955: 15, pl. 2 (figs 1–3), text-figs 3–4. Upper Albian of Nigeria. Casey (1961b: 139) has suggested that this species is 'a completely new development whose relationship to the *Aconeceratidae* is doubtful. Possibly it is congeneric with the *Aconeceras*? described by Haas (1942: 165) from the Upper Albian of Angola'.

? Genus *Eofalciferella* Brunnenschweiler, 1959

- Type species: *Eofalciferella condoni* Brunnenschweiler, 1959, by original designation.
- Eofalciferella condoni* Brunnenschweiler, 1959: 13, pl. 1 (figs. 3–4). Aptian of Australia. The only illustrations of this species are pencil sketches of the unique holotype, a crushed specimen from the Windalia Radiolarite. The species and genus are best treated as *nomen dubia*; Casey (1961b: 131) implies in his discussion of the genus that its affinities may be with *Sanmartinoceras*.

Family Binneyitidae Reeside, 1927

Genus *Falciferella* Casey, 1954

- Type species: *Falciferella milbournei* Casey, 1954, by original designation.
- Falciferella milbourni* Casey, 1954: 274, pl. 7 (figs 1–5), text-fig. 3. Middle Albian of southern England.
- Falciferella malandiandrensis* Collignon, 1962: 32, pl. 229 (fig. 975). Upper Aptian of Madagascar. This species is keeled to a diameter of approximately 45 mm. It may be an *Aconeceras*, although Collignon (1962) indicates that it has a *Falciferella*-like suture.

Genus *Doridiscus* Casey, 1961

- Type species: *Doridiscus rotulus* Casey, 1961, by original designation.
- Doridiscus rotulus* Casey, 1961b: 139, pl. 26 (fig. 8a–b), text-fig. 44c–e. Low Upper Aptian of southern England.
- Doridiscus* sp. nov. indet? Casey, 1961b: 140, text-fig. 44f. Upper Lower Aptian of southern England.

Genus *Nothodiscus* Casey in Collignon, 1962

Type species: *Nothodiscus planus* Casey, in Collignon, 1962, by original designation.

Nothodiscus planus Casey in Collignon, 1962: 32, pl. 229 (fig. 976). Upper Aptian of Madagascar.

Genus *Borissiakoceras* Arkhangelsky, 1916

Type species: *Borissiakoceras mirabile* Arkhangelsky, 1916: 55, pl. 8 (figs 2–3), Lower Turonian of Turkestan. Kennedy & Juignet, 1973: 900, text-figs 1–2, Middle Cenomanian of France.

Borissiakoceras compressum Cobban, 1961: 747, pl. 87 (figs 19–33); pl. 89 (figs 1–9), text-fig. 4a–k. Middle Cenomanian of the United States Western Interior.

Borissiakoceras reesidei Morrow, 1935: 463, pl. 49 (fig. 7a–b), pl. 50 (fig. 5), text-fig. 8. Cobban, 1961: 749, pl. 88 (figs 1–14), text-fig. 3h–k. Middle Cenomanian of the United States Western Interior.

Borissiakoceras orbiculatum Stephenson, 1955: 64, pl. 6 (figs 1–4). Cobban, 1961: 750, pl. 88 (figs 15–41), text-fig. 5a–f. Middle/Upper Cenomanian of Texas and the United States Western Interior.

Borissiakoceras cf. *B. orbiculatum* Stephenson, 1955; Cobban 1961: 753, pl. 89 (figs 10–14), text-fig. 5g, i. Uppermost Cenomanian of the Black Hills, United States Western Interior.

Borissiakoceras inconstans Cobban & Gryc, 1961: 187, pl. 38 (figs 30–37), text-fig. 2i–l. Latest? Cenomanian of Alaska.

Borissiakoceras ashurkoffae Cobban & Gryc, 1961: 188, pl. 38 (figs 38–43), text-fig. 2j–k, m. Lower Turonian of Alaska.

Borissiakoceras (?) sp. Wright, 1963: 602, pl. 89 (fig. 5). Middle Cenomanian of Bathurst Island, Australia.

Borissiakoceras ? sp. Lower Cenomanian of Sarthe, France (Sorbonne collections).

Borissiakoceras sp. Kennedy & Klinger, 1978. (See p. 116.) Middle Cenomanian of Zululand.

Genus *Johnsonites* Cobban, 1961

Type species: *Johnsonites sulcatus* Cobban, 1961, by original designation.

Johnsonites sulcatus Cobban, 1961: 743, pl. 87 (figs 1–18), text-fig. 3a–g. Middle Cenomanian of Wyoming and Colorado in the United States Western Interior.

? *Johnsonites* sp., the original of Stephenson's (1952: 198, pl. 45 (figs 5–6)) *Euhoplites* ? sp. from the Middle Cenomanian of Texas may also belong to this genus.

Genus *Binneyites* Reeside, 1927

Type species: *Binneyites parkensis* Reeside, 1927, by original designation.

Binneyites parkensis Reeside, 1927: 5, pl. 3 (figs 1–10). Cobban, 1961: 754, pl. 89 (figs 32–37), text-fig. 5s, t. Coniacian of Wyoming and Utah in the United States Western Interior.

Binneyites carlilensis Cobban, 1961: 755, pl. 89 (figs 15–22), text-fig. 5h, j–m. Mid-Turonian of South Dakota and Wyoming in the United States Western Interior.

Binneyites aplatus (Morrow), 1935: 465, pl. 49 (fig. 5), pl. 50 (fig. 6), text-fig. 7. Mid-Turonian of Kansas in the United States Western Interior.

Binneyites rugosus Cobban, 1961: 756, pl. 89 (figs 26–31), text-fig. 5n–p.

The Engonoceratidae gen. et sp. nov. of Henderson, 1973: 106, fig. 14 (no. 8), text-fig. 15, is either a *Borissiakoceras* or *Binneyites* of Turonian age.

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We thank Dr H. W. Ball, Dr M. K. Howarth and Mr D. Phillips of the British Museum (Natural History), Dr R. Casey and Mr C. J. Wood (Institute of Geological Sciences), Mr C. W. Wright and Dr M. R. Cooper (Oxford), for their advice and useful discussions. The assistance of the staff of the Geological Collections at Oxford University Museum, and South African Museum, Cape Town, is gratefully acknowledged as is the financial support of the Trustees of the Sir Henry Strakosh Bequest, the Royal Society, and Natural Environment Research Council.

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Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

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Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierii Philippi, 1861: 87.

Leda bicuspidata: Nickles, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

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FISCHER, P.-H. 1948. Données sur la résistance et de le vitalité des mollusques. *J. Conch.*, Paris 88: 100-140.

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A NEW GENUS AND SPECIES OF
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A NEW GENUS AND SPECIES OF THE PENAEOID FAMILY SOLENOCERIDAE (CRUSTACEA, DECAPODA) FROM SOUTH-EAST AFRICAN WATERS

By

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(With 1 figure and 1 table)

[MS accepted 31 October 1978]

ABSTRACT

A new genus, *Cryptopenaeus*, is proposed for a new solenocerid species, *Cryptopenaeus catherinae*, which is described and illustrated. The new genus is related to *Hymenopenaeus* and *Haliporoides* formerly belonging to the genus *Hymenopenaeus*, *sensu lato*. *C. catherinae* has so far been found only in three localities off southern Mozambique at depths of 310–500 metres.

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INTRODUCTION

In June 1969, while collecting penaeoid shrimps aboard a trawler operating in deep water off southern Mozambique, one male specimen representing a new genus and species was caught in 350 metres of water. Further male specimens were subsequently found in the same area in June 1973, and the only female available was caught in September 1976 at a depth of 500 metres.

All specimens were caught together with the commercially important pink or knife prawn *Haliporoides triarthrus*, as well as the less common *Aristeomorpha foliacea* and *Penaeopsis balssi*.

Genus *Cryptopenaeus* gen. nov.

Diagnosis

Body robust; carapace elongate; integument firm. Rostrum short, not reaching distal margin of first antennular segment; ventral margin moderately convex; armed only with dorsal teeth; epigastric tooth and first rostral separated by interval equal to or only slightly greater than that between first and second rostral teeth. Orbital, suprahepatic and branchiostegal spines absent; antennal, postorbital, hepatic and pterygostomial spines present; cervical sulcus deep, long but not reaching mid-dorsum of carapace; hepatic sulcus deep and long, bending anteroventrally from horizontal posterior part and almost reaching

base of pterygostomian spine; orbito-antennal groove shallow and wide; branchiocardiac carina distinct but not sharp; mid-dorsal abdominal carina present on segments two to six. Telson with pair of short fixed spines; no movable marginal spines. Prosartema narrow, long, extending beyond end of eye. Antennular flagella similar, subcylindrical and equal to, or slightly longer than, carapace. Mandibular palp two jointed; articles subequal in length, distal one narrower than basal and tapering to rounded apex. Exopodites on all maxillipeds and pereopods. Lateral ramus of uropod with very small, blunt distolateral spine. Petasma with ventrolateral lobule entirely occupied by ventral costa and distally free from dorsolateral lobule; both ventrolateral and dorsolateral lobules heavily sclerotized; appendix masculina and appendix interna present. Thelycum simple, of open type. Podobranch on maxilliped II only; epipodites on maxillipeds II and III and on pereopods I–IV.

Type species

Cryptopenaeus catherinae sp. nov.

Etymology

The generic name is derived from the prefix *crypto*, from the Greek *kryptos* meaning hidden, in combination with the generic name *Penaeus*, denoting the fact that this shrimp has been hidden from science until now; gender masculine.

Taxonomic status and comments

From the works of Bate (1881, 1888), Bouvier (1906), and Burkenroad (1936), it is clear that the generic complex forming the then accepted subfamily Solenocerinae presented many taxonomic difficulties. This subfamily consisted of three genera: *Solenocera*, shrimps with concave antennular flagella (Lucas 1849; Wood-Mason & Alcock 1891; Barnard 1950); *Haliporus*, shrimps with subcylindrical antennular flagella and movable lateral spines on the telson anterior to fixed pair (Bate 1881; Kensley 1968); and *Hymenopenaeus*, shrimps with subcylindrical antennular flagella and lacking lateral spines on the telson (Smith 1882; Wood-Mason & Alcock 1891; Barnard 1950).

It is apparent from the literature, however, that Burkenroad (1936) was somewhat unhappy with the taxonomic status of *Hymenopenaeus* and went to the point of dividing the genus into four superspecies ‘. . . according to the presence or absence of branchiostegal or pterygostomian spines and to the nature of the postrostral armature’. Pérez Farfante (1977) revised the subfamily and, besides proposing that the subfamilies hitherto accepted should be elevated to the category of families of the superfamily Penaeoidea, divided *Hymenopenaeus* into five genera partly based on the superspecific groups elaborated by Burkenroad (1936). In doing so Pérez Farfante takes into consideration the ‘. . . shape of the antennular flagella and rostrum, proportions of the carapace, number and comparative size of the articles of the mandibular palp, presence or absence of certain carinae on the carapace, relative dimensions of the posterior

two pairs of pereopods, location of the distolateral spine of the lateral ramus of the uropod, structure of the petasma and degree of development of the arthrobranchia on somite VII', as well as those characteristics originally used by Burkenroad.

The system presented is very comprehensive and covers the previously known species extremely well. However, whereas the six specimens caught in southern Mozambique belong clearly to the family Solenoceridae and would have fitted into the genus *Hymenopenaeus sensu lato*, they do not belong to any of the five genera established by Pérez Farfante (1977), and have therefore been placed in a new genus, *Cryptopenaeus*.

Table 1 sets out the similarities and differences between *Cryptopenaeus* and the other five genera, *Hymenopenaeus*, *Haliporoides*, *Pleoticus*, *Hadropenaeus*, and *Mesopenaeus*. The new genus is closely allied to *Hymenopenaeus* and *Haliporoides* but differs from the former in the arrangement of the rostral teeth, the absence of branchiostegal spines, the presence of a mid-dorsal carina on abdominal segments 2 and 3 and also by the short rostrum with a strongly convex ventral margin. *Cryptopenaeus* differs from *Haliporoides* in the arrangement of the rostral teeth, presence of a dorsal carina on the second abdominal segment, by the absence of a suprahepatic spine and by the short rostrum with a strongly convex ventral margin. The petasma of *Cryptopenaeus* differs from that of the other five genera in having the ventrolateral lobule entirely occupied by the ventral costa.

Cryptopenaeus catherinae sp. nov.

Fig. 1

Material

Holotype: SAM-A16148 in the South African Museum, Cape Town, ♂, 46.7 mm carapace length, caught off Cape Santa Maria in southern Mozambique (26°06'S 33°08'E) at a depth of 350 metres, on 16 December 1969.

Allootype: SAM-A16149 in the South African Museum, Cape Town, ♀, 63.2 mm carapace length, caught off Monte Bello in southern Mozambique (25°00'S 35°21'E) at a depth of 500 metres, in September 1976.

Paratypes: 4 ♂♂, 44.5–47.7 mm carapace length, caught off southern Mozambique at a depth of 310 metres, in June 1973. One male paratype is in the National Museum of Natural History in Washington, D.C., and the remaining three will be sent to the British Museum (Natural History).

Description

Rostrum. Slightly downwardly directed, reaching to or just beyond end of first antennular segment; ventral margin convex; rostral teeth $\frac{7-8}{0}$; epigastric and three other teeth situated behind postorbital margin of carapace; adrostral carina short, just reaching postorbital margin; postrostral carina very well developed, long, almost reaching posterior margin of carapace and with conspicuous notch behind epigastric tooth; median groove absent.

TABLE I
Characteristics distinguishing *Cryptopenaeus* gen. nov. from the five closely related genera

	<i>Hymenopenaeus</i>	<i>Haliporoides</i>	<i>Pleoticus</i>	<i>Hadropenaeus</i>	<i>Mesopenaeus</i>	<i>Cryptopenaeus</i>
Epigastric and rostral teeth ..	Epigastric and 1st rostral teeth separated from 2nd	Epigastric separated from 1st rostral tooth	Separated by regularly decreasing intervals	Separated by regularly decreasing intervals	Separated by regularly decreasing intervals	Separated by regularly decreasing intervals
Abdominal dorsal carina ..	4-6	3-6	1-6 or 3-6	3-6	3-6	2-6
Branchiostegal spine ..	Present	Absent	Present or absent	Present	Absent	Absent
Pterygostomian spine ..	Present or absent	Present	Absent	Absent	Absent	Present
Orbital spine ..	Absent	Absent	Present	Absent	Present	Absent
Suprahepatic spine ..	Absent	Present	Absent	Absent	Absent	Absent
Branchiocardiac carina ..	Present	Present	Absent	Absent	Absent	Present
Submarginal carina ..	Present	Present	Present	Absent	Absent	Present
Ventral margin of rostrum ..	Straight	Long, straight to concave	Straight to concave	Strongly convex	Strongly convex	Short and convex

Carapace. Uniformly glabrous and lightly punctate; gastrofrontal and postocular grooves and horizontal suture absent; no supra-orbital spine; cervical sulcus and carina very well developed and long but not reaching dorsal midline; cervical carina terminating anteroventrally in prominent hepatic spine; gastro-orbital carina absent; postorbital spine prominent; antennal spine present but relatively small; antennal carina absent; orbito-antennal groove restricted to wide depression extending from below postorbital spine to below hepatic spine; hepatic carina sharp, anteroventrally directed and situated just anterior and below hepatic spine; hepatic sulcus wide and deep; extending posteriorly below hepatic spine; branchiocardiac carina distinct but not very sharp. Branchiostegal spine absent; pterygostomian spine prominent and sharp; submarginal carina long and sharp; no vertical suture or carina.

Antennule. Flagella subequal in length; about 2,5 times length of antennular peduncle; subcylindrical; mesial flagella twice as thick as lateral flagella; prosartema flexible with pointed apex, reaching just beyond distal end of first antennular peduncle, copiously provided with long setae; stylocerite sharply pointed distally, straight and reaching just beyond end of eye or to end of first antennular article; distolateral spine prominent and long; parapenaeid spine absent.

Scaphocerite. Distolateral spine reaching just beyond distal end of antennular peduncle; apex of lamella extending beyond distolateral spine; basicerite with single broad blunt tooth distally.

Mandibular palp. Reaching to about basal one-third of carapocerite; proximal article 1,8 times as long as wide; distal article subequal to proximal, tapering to rounded apex.

Maxilliped III. Endopodite not exhibiting sexual dimorphism; reaching distal end of scaphocerite; exopodite short, reaching less than half-way along merus of endopodites; epipodite present.

Pereiopods. Exopodites present on all pereiopods, well developed, longest on first pereiopod and shortest on fifth; epipodites present on pereiopods I–IV; basipodites of first, second and third with prominent spines; ischial spine present on first pereiopod only; distinct coxal spine on fifth pereiopod. Pereiopod IV reaching to apex of mandibular palp; pereiopod V reaching to distal end of antennular peduncle. Extended laterally lengths of pereiopods in ascending order are: first, second and fourth, third and fifth.

Abdomen. Uniformly glabrous; mid-dorsal carina present from posterior half of second segment to end of sixth where it terminates in short spine; short vertical groove on pleura of first segment; lateral carinae absent.

Telson. Slightly longer than sixth segment; about as long as mesial ramus of uropod; median groove deep, occupying only anterior half of telson; apical spine somewhat blunt; pair of inconspicuous, very short, fixed subapical spines present; movable marginal spines lacking.

Thelycum. Simple open structure; anterior portion formed by vertical posterior face of sternite between fourth pereiopods; posterior face with short

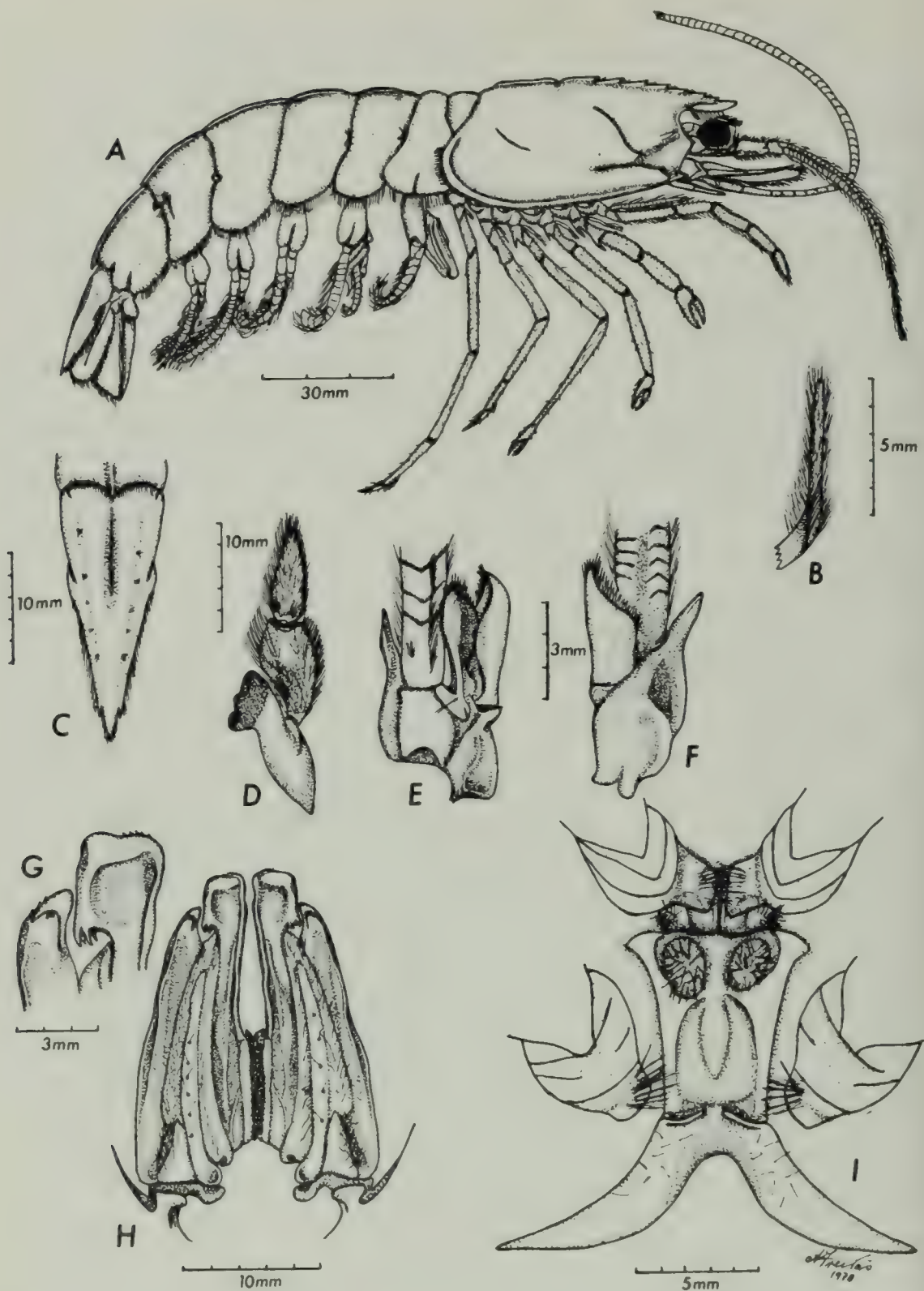


Fig. 1. *Cryptopenaeus catherinae* sp. nov. A. Lateral view, holotype ♂ 46,7 mm carapace length. B. Right prosartema. C. Telson. D. Left mandibular palp, ventral view. E. Left appendix masculina and interna, ventral view. F. Appendix masculina, dorsal view. G. Distal subquadrate process of right half of petasma. H. Petasma, ventral view. I. Thelycum.

median groove and low lateral ridges; covered with short setae and obscured by coxal protuberances of fourth pereiopods. Posterior portion (between fifth pereiopods) consisting of elongate plate; broad central ridge occupying slightly more than anterior two-thirds of plate; well-defined lateral ridges extending from posterior sternal process to anterior margin of somite; two suboval, setose, boss-like structures present between anterior third of lateral ridges and median ridge; anterior margin of posterior sternal process interrupted by deep median sulcus.

Petasma. Simple and very slightly involuted; dorsomedian lobule about two-fifths of total length of petasma; entirely united along midline; ventro-median lobule elongate and subtriangular; inner membranous section folded slightly on itself; heavily sclerotized central ridge running length of lobule terminating distally in thick subquadrate process; distal margin smooth; proximolateral angle of quadrate process beak-like with four or five blunt teeth; ventral face of process concave; dorsal face convex; dorsolateral lobule elongate and subtriangular; apex situated under proximolateral angle of distal ventro-median process; lower inner angle forms small proximal process; ventral surface sparsely covered with long setae; ventral costa (occupying entire ventrolateral lobule) extending along lateral margin of petasma reaching half way into distal ventromedian process; apex free and bi-lobed; dorsal lobe longer than ventral lobe; ventral lobe with one to four minute teeth.

Appendix masculina. Dorsally convex, ventrally concave, roughly trapezoid in shape; distal margin with row of short, stout setae; appendix interna subequal in length to appendix masculina, half fitting into concave face of latter; elongate with concave median surface; apex with short stout setae. Basal segment of endopodite of pleopod II as wide as long, its distolateral portion concave, subtriangular and produced into long, blunt spur.

Colour in life. Body generally red, carapace with broad white stripe running from below hepatic sulcus to almost posterior margin of carapace on each side; this stripe wider in posterior half of carapace; on abdominal segments brighter red patch running anteroventrally on each pleuron; distinct white longitudinal stripe on dorsal carina of abdominal segments 4–6; telson and uropods pinkish white becoming red along posterior edges; lateral margins of scaphocerite red; rostral crest and pereiopods pinkish white; basal segments of pleopods grey to white; pleopodal endopodites greyish white becoming bright red distally; marginal setae of pleura, pleopods and uropods orange while those of scaphocerite and antennules white.

Distribution

Known only from the type locality.

Ecological notes

All the specimens were collected from the same general area, namely the Limpopo Bight in southern Mozambique. This is an important fishing ground

where the main species of interest are the spiny lobster, *Palinurus delagoae*, caught in about 280–350 metres, the langoustine, *Nephrops andamanicus*, trawled in 320–380 metres, and the pink or knife prawn, *Haliporoides triarthrus*, found in 300–500 metres.

In this area, the continental slope is relatively gentle down to 500 metres after which it drops very steeply to about 3 000 metres. The substrate consists of muddy sand to sandy mud and the temperature at 300–500 metres depth recorded in April and September 1964 was 11–13°C (Instituto Hidrográfico Lisbon 1965, 1967).

Although *Cryptopenaeus catherinae* has so far been found only in the type locality, it seems feasible to expect that, as its associate species, *Haliporoides triarthrus*, *Aristeomorpha foliacea* and *Penaeopsis balssi* are found off the coast of Natal, the distribution of *C. catherinae* could possibly extend southward as well.

ACKNOWLEDGEMENTS

I wish to thank the Fisheries Development Corporation and the South African Association for Marine Biological Research for their financial and administrative assistance; Dr Isabel Pérez Farfante of the Systematics Laboratory, National Marine Fisheries Service, Washington D.C., U.S.A., for having checked the identity of this species and for the meticulous way in which she read and criticized my manuscript; Professor A. E. F. Heydorn, Director of the Oceanographic Research Institute, Durban, for his encouragement and for his criticism of the manuscript; Dr P. F. Berry for reading and criticizing the paper; and finally my wife, after whom this species is named, for her encouragement, patience and understanding.

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Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierii Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

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ANTÓNIO J. DE FREITAS

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(continued inside back cover)

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Cape Town Kaapstad

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TYPE SPECIMENS OF HYDROIDA (COELENTERATA) IN THE SOUTH AFRICAN MUSEUM

By

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[MS. accepted 31 October 1978]

ABSTRACT

A list is given of seventy-nine types of Hydroida housed in the South African Museum, including spirit material, whole mounts and microscope sections.

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INTRODUCTION

This paper lists the type holdings of Hydroida in the South African Museum, and includes not only material preserved in alcohol, but also whole mounts and sections prepared for microscopic examination.

The arrangement of families, genera and species is the same as that used by Millard (1975).

Each specimen has a South African Museum registered number (prefixed by the letters SAM-H), and in most cases a second number is quoted too, which is that of the collector's catalogue. For the latter the following abbreviations are used:

- UCT University of Cape Town; material from the Ecological Survey of the intertidal rocky shore, the estuaries and the benthic region of the South African seas. It should be noted that most of the U.C.T. collection of hydroids is now housed in the South African Museum.
- PF Material collected by the old Government Survey vessel, the R.S. *Pieter Faure*. The positions given in the *Pieter Faure* catalogue were not very reliable, but have been converted here as accurately as possible into latitude/longitude positions.
- MD Duplicate material from the Museum National d'Histoire Naturelle, Paris, collected during the cruise MD.03 of the *Marion-Dufresne* (Millard 1977a).
- MT Duplicate material from the collection of the Musée Royal de l'Afrique Centrale, Tervuren, Belgium, collected by J. Bouillon (Millard & Bouillon 1973, 1974, 1975).

- SM Material collected by the R.V. *Meiring Naude* off the east coast of South Africa (Millard 1977b).
- TME Duplicate material from the Universitetets Zoologiske Museum, Copenhagen, collected during Th. Mortensen's Java-South Africa Expedition, 1929-1930 (Millard 1968).

SPECIES LIST

Suborder ATHECATA

Family Myriothelidae

Monocoryne minor Millard, 1966: 435, fig. 1.

Holotype: SAM-H417 (UCT SCD 215C). One fertile specimen detached from substratum.

Locality: Agulhas Bank, 34°03'S 25°58'E; 78 m; 25 November 1960.

Collected by: University of Cape Town.

Myriothela tentaculata Millard, 1966: 437, fig. 2.

Holotype: SAM-H418 (UCT WCD 7Q). One male individual on encrusting bryozoan.

Locality: Off west coast of Cape Peninsula, 34°09,3'S 18°17,5'E; 43 m; 24 March 1959.

Paratype: SAM-H2915 (UCT WCD 7Q). Microscope sections of male individual; locality as holotype.

Collected by: University of Cape Town.

Family Corynidae

Bicorona elegans Millard, 1966: 441, fig. 3.

Holotype: SAM-H419 (UCT SB 161X). Rich male and female colonies; plus one whole mount; plus microscope sections.

Locality: Saldanha Bay, 33°02,5'S 18°02'E; littoral; September 1957.

Collected by: University of Cape Town.

This is the type species of the genus *Bicorona* Millard, 1966.

Family Eudendriidae

Eudendrium deciduum Millard, 1957: 184, fig. 2.

Holotype: SAM-H98 (UCT FAL 52V). Male and female colonies; plus one whole mount; plus microscope sections.

Locality: False Bay, from 34°09,3'S 18°49,6'E to 34°09'S 18°50,1'E; 18 m; 25 June 1952.

Collected by: University of Cape Town.

Eudendrium ritchiei Millard, 1975: 87, fig. 30.

Holotype: SAM-H1803. Abundant male and female colonies; plus two whole mounts.

Locality: Saunders Rocks, Sea Point; littoral; 5 March 1973.

Collected by: N. A. H. Millard.

Family **Bougainvilliidae**

Clavopsella quadrangularia Thiel, 1962: 227, figs 1-28.

= *Clavopsella navis*: Millard, 1975: 100, fig. 34A-D. (See also *Rhizorhagium navis*.)

Schizoparatypes: SAM-H1774, H1775 (presented by Dr H. Thiel 1972).

Locality: Kiel Canal.

Rhizorhagium navis Millard, 1959b: 244, fig. 2.

= *Clavopsella navis*: Millard, 1975: 100, fig. 34A-D. (See also *Clavopsella quadrangularia*.)

Holotype: SAM-H124 (UCT SH 429B). Male and female colonies on weed and other hydroids; plus one whole mount.

Locality: Cape Town docks, on ship's hull; 10 February 1958.

Collected by: N. A. H. Millard.

Silhouetta uvacarpa Millard & Bouillon, 1973: 25, fig. 3A-D, pls 2-3.

Schizoholotype: SAM-H2916 (MT 2664). Three whole mounts only, bearing medusa buds.

Locality: Silhouette Island, Seychelles; 1966.

Collected by J. Bouillon.

This is the type species of the genus *Silhouetta* Millard & Bouillon, 1973.

Family **Hydractiniidae**

Clavactinia multitentaculata Millard, 1975: 106, fig. 35C-G.

As *Hydractinia* sp.: Millard, 1968: 255.

Holotype: SAM-H389 (PF station 10724). Male colony on shell of gastropod *Melapium lineatum* (Lamarck), occupied by hermit *Dardanus arrosor* (Herbst); plus two whole mounts; plus microscope sections.

Locality: off Natal, approx. 29°54'S 31°11'E; 99 m; 14 December 1900.

Collected by: R.S. Pieter Faure.

Hydractinia altispina Millard, 1955: 215, fig. 1.

Lectotype: SAM-H87 (UCT F 274). Male colony on gastropod *Thais squamosa* (Lamarck); plus microscope sections.

Locality: St James, False Bay; littoral; 1 August 1936.

Paralectotypes: SAM-H88 (UCT CP 258). Infertile colonies on two specimens of *Thais squamosa*; plus one whole mount; St James, False Bay; littoral; April, 1944.

SAM-H89 (UCT B 92). Colonies with very young gonophores on two specimens of *Thais squamosa*; Lambert's Bay; littoral; 30 July 1938.

Collected by: University of Cape Town.

Hydractinia canalifera Millard, 1957: 179, fig. 1.

Holotype: SAM-H97 (UCT CP 332). Female colony on weed; plus one whole mount; plus microscope sections.

Locality: Clovelly, False Bay; littoral; 23 August 1949.

Collected by: N. A. H. Millard.

Hydractinia diogenes Millard, 1959a: 305, fig. 2.

Holotype: SAM-H123 (UCT MOR 51H). Male and female colonies on five gastropod shells occupied by hermits *Diogenes costatus* (Fabricius); plus three whole mounts; plus microscope sections.

Locality: off mouth of Rio Coche, Mozambique; 3–5 m; 21 January 1954.

Collected by: University of Cape Town.

Hydractinia kaffraria Millard, 1955: 217, fig. 2.

Lectotype: SAM-H90 (UCT BRE 111A). Female colony on gastropod *Nassarius kraussianus* (Dunker).

Locality: Breede River estuary; 3 February 1952.

Paralectotypes: SAM-H92 (UCT SUN 3N). Colonies on five specimens of *Nassarius kraussianus*; plus one whole mount; Sunday's River estuary; 7 January 1950.

SAM-H91 (UCT HAM 3Q). Microscope sections of female colony; Keiskama River estuary, The Haven; 9 January 1950.

Collected by: University of Cape Town.

Hydractinia marsupialia Millard, 1975: 113, fig. 38.

Holotype: SAM-H1854 (UCT TB 13). Female colony on gastropod *Nassarius speciosus* Adams; plus microscope sections of male and female colonies.

Locality: Table Bay; 9–18 m; 4 August 1946.

Paratypes: SAM-H1855 (UCT TB 14 plus 15). Nine colonies, male and female, on *Nassarius speciosus*; plus one whole mount; Table Bay; 17–20 m; 25 October 1946 and 11 February 1947.

Collected by: University of Cape Town.

Family Cytaeidae

Podocoryne nassa Millard, 1959a: 307, fig. 3.

= *Cytaeis nassa*: Rees, 1962: 390, figs 8–9, pl. 11.

Holotype: SAM-H122 (UCT IN 112). Fertile colonies on two shells of gastropod *Nassarius fenestratus* Marrat; plus one whole mount; plus microscope sections.

Locality: Punta Torres, Inhaca Island, Mozambique; littoral; 18 September 1955.

Collected by: University of the Witwatersrand.

Suborder THECATA

Family Campanulinidae

Aequorea africana Millard, 1966: 461, fig. 8.

Holotype: SAM-H420 (UCT MB 70G). Fertile colony on empty gastropod shell; plus two whole mounts.

Locality: Mossel Bay, 34°08,9'S 22°07,9'E; 18 m; 19 January 1956.

Collected by: University of Cape Town.

Egmundella amirantensis Millard & Bouillon, 1973: 40, fig. 5A–D.

Schizoholotype: SAM-H2917 (MT 2665). One whole mount only of fertile material.

Locality: Amirante Island, Seychelles; 1966.

Collected by: J. Bouillon.

Lineolaria gravierae Millard, 1975: 134, fig. 43H.

As *Lineolaria* sp.: Gravier, 1970: 144, figs 11, 13A. Millard & Bouillon, 1974: 22, fig. 2D.

Schizoholotype: SAM-H1955. One whole mount (infertile) only.

Locality: Barreira Vermelha, Inhaca, Mozambique, 26°02'S 32°54'E; 1969.

Collected by: J. Bouillon.

Lovenella chiquitita Millard, 1957: 198, fig. 7.

Holotype: SAM-H103 (UCT FAL 288J). One whole mount only of fertile colony epizootic on *Eudendrium deciduum* Millard.

Locality: False Bay, 34°09,6'S 18°49,8'E; 18 m; 15 October 1897.

Collector unknown.

Paratypes: SAM-H104 (UCT FB 131K). Two whole mounts (infertile), one epizootic on *Sertularella polyzonias falsa* Millard; False Bay, 34°09'S 18°26,7'E; 5–8 m; 13 December 1949.

SAM-H105 (UCT FAL 108O). One whole mount (infertile) epizootic on *Sertularella polyzonias falsa*; False Bay, 34°09,3'S 18°51'E; 8–12 m; 23 January 1953.

Collected by: University of Cape Town.

Family Haleciidae

Halecium dufresneae Millard, 1977a: 8, fig. 2A–D.

Schizoholotype: SAM-H2785 (MD station 26/63). Fragments of female colony; plus one whole mount.

Locality: Crozet Island, Chenal des Orques, 46°21,5'S 51°55'E; 230 m; 20 April 1974.

Collected by: R.V. Marion Dufresne.

Halecium inhacae Millard, 1958: 168, fig. 1.

Holotype: SAM-H114 (UCT IN 140H). Female colony on weed; plus two whole mounts.

Locality: Inhaca Island, Mozambique, east shore rocks; 20 July 1956.

Collected by: University of the Witwatersrand.

Halecium parvulum, var. *magnum* Millard, 1957: 190, fig. 4B–O.

Since incorporated in *Halecium delicatulum* Coughtrey, 1876 (large form).

Holotype: SAM-H99 (UCT FAL 274R). Male and female colonies; plus three whole mounts.

Locality: False Bay, 34°10,9'S 18°27,2'E; 14–17 m; 21 September 1954.

Collected by: University of Cape Town.

Paratypes: SAM-H100 (UCT FAL 159L). Infertile colony; plus one whole mount; False Bay, 34°12,5'S 18°28'E; 0–3 m; 21 April 1953.

Collected by: University of Cape Town.

SAM-H11 (PF station 405). Male colony; plus two whole mounts; off Buffels Bay, False Bay; depth unknown; 8 October 1898.

SAM-H30 (PF station 16287). Female colony; plus two whole mounts; off Cape Point, approx. 34°20'S 18°32'E; 59 m; 9 December 1902.

Collected by: R.S. Pieter Faure.

Hydrodendron sympodiformis Millard & Bouillon, 1974: 25, fig. 5.

Schizoholotype: SAM-H1732 (MT station InPT 42). Part of a female colony on weed; plus one whole mount.

Locality: Punta Torres, Inhaca, Mozambique; August 1969.

Collected by: J. Bouillon.

Family Lafoeidae

Hebella furax Millard, 1957: 200, fig. 8.

Holotype: SAM-H34 (PF station 18293). Infertile colony parasitic and epizootic on *Lytocarpus filamentosus* (Lamarck); plus two whole mounts.

Locality: False Bay, approx. 34°05,5'S 18°39'E; 15–18 m; 7 December 1903.

Collected by: R.S. Pieter Faure.

Paratype: SAM-H106 (UCT FAL 58Y). Infertile colony on *Lytocarpus filamentosus*; one whole mount only; False Bay, 34°09,4'S 18°50,4'E; 12 m; 25 June 1952.

Collected by: University of Cape Town.

Hebella muscensis Millard & Bouillon, 1975: 10, fig. 3A–B.

Schizoholotype: SAM-H2918 (MT station SEY 20K). Two whole mounts only of fertile colony epizootic on *Syntheicum* sp.

Locality: Anse la Mouche, Seychelles; 1972.

Collected by: J. Bouillon.

Hebella urceolata Millard, 1964: 11, fig. 2A.

Since incorporated in *Hebella scandens* (Bale, 1888)

Holotype: SAM-H410 (UCT SCD 154H). Infertile colony epizootic on *Halecium beanii* (Johnston); plus one whole mount.

Locality: Agulhas Bank, 34°03'S 25°59'E; 84 m; 25 November 1960.

Collected by: University of Cape Town.

Scandia tubitheca Millard & Bouillon, 1975: 10.

As *Scandia corrugata*: Millard & Bouillon, 1973: 60 (*pro parte*), fig. 8D–F.

Schizoholotype: SAM-H2919 (MT station Am 1P). Male colony epizootic on *Syntheicum dentigerum* Jarvis; two whole mounts only.

Locality: Amirante Island, Seychelles; 30 August 1966.

Collected by: J. Bouillon.

Zygophylax cornucopia Millard, 1955: 219, fig. 3.

= *Hydrodendron cornucopia*: Millard, 1973: 33, fig. 6A–E (transferred to Haleciidae).

Holotype: SAM-H93 (UCT FB 131B). Male and female colonies epizootic on *Antennella quadriaurita* Ritchie; plus one whole mount.

Locality: False Bay, 34°09'S 18°26,7'E; 5–8 m; 13 December 1949.

Paratypes: SAM-H94 (UCT TB 1B). Infertile colonies epizootic on *A. quadriaurita*; plus one whole mount; Table Bay, 33°47,5'S 18°24,3'E; 19–20 m; 11 February 1947.

SAM-H95 (UCT FAL 78S). Fertile colonies epizootic on *A. quadriaurita*; plus one whole mount; False Bay, several positions; 4–17 m; 19 August 1952–23 September 1954.

SAM-H96 (UCT FAL 217N); one whole mount of infertile colony epizootic on *A. quadriaurita*; False Bay, 34°07'S 18°32,5'E; 18 m; 9 September 1953.

Collected by: University of Cape Town.

Zygophylax crozetensis Millard, 1977a: 15, fig. 4.

Schizoholotype: SAM-H2779 (MD station 26/64). Part of a large fertile colony; plus one whole mount.

Locality: Crozet Island, Chenal des Orques, 46°24'S 51°59'E; 180 m; 20 April 1974.

Collected by: R.V. Marion Dufresne.

Zygophylax enigmatica Millard, 1964: 19, fig. 5A–F.

= *Hydrodendron gracilis* (Fraser, 1914): Millard, 1973: 33, fig. 6F–G (transferred to Haleciidae).

Holotype: SAM-H411 (UCT WCD 12E); female colony epizootic on *Nemertesia ramosa* Lamouroux; two whole mounts only.

Locality: off Cape Town, 34°09,4'S 18°16,5'E; 75 m; 24 March 1959.

Collected by: University of Cape Town.

Zygophylax geminocarpa Millard, 1958: 177, fig. 4D–G.

Holotype: SAM-H59 (PF station 12308). About eight fertile stems; plus two whole mounts.

Locality: off Natal, approx. 30°53'S 30°28'E; 66 m; 14 March 1901.

Collected by: R.S. Pieter Faure.

Zygophylax inconstans Millard, 1977b: 117, fig. 5.

Holotype: SAM-H1975 (SM station 23J). A fertile, tangled colony on a bryozoan; plus one whole mount.

Locality: off Natal, 27°44,4'S 32°42,8'E; 400–450 m; 26 May 1975.

Collected by: R.V. Meiring Naude.

Zygophylax infundibulum Millard, 1958: 180, fig. 4B–C.

Holotype: SAM-H36 (PF station 10781). Several infertile stems; plus two whole mounts.

Locality: off Natal, approx. 29°53'S 31°11'E; 155 m; 17 December 1900.

Collected by: R.S. Pieter Faure.

Family Campanulariidae

Campanularia laminacarpa Millard, 1966: 472, fig. 12E–K.

Holotype: SAM–H421 (UCT TRA 32A). A female colony epizootic on *Thyroscyphus aequalis* Warren; plus two whole mounts.

Locality: Agulhas Bank, 34°49'S 20°21,5'E; approx. 91 m; 9 November 1947.

Collected by: commercial trawler.

Campanularia morgansi Millard, 1957: 195, fig. 6.

Holotype: SAM–H24 (PF station 15675). Female colonies epizootic on *Corhiza scotiae* (Ritchie) and *Sertularella arbuscula* (Lamouroux); plus one whole mount.

Locality: False Bay, approx. 34°28'S 18°32'E; 73 m; 9 October 1902.

Collected by: R.S. Pieter Faure.

Paratypes: SAM–H7 (PF station 351). Infertile colony epizootic on *Salacia articulata* (Pallas); plus one whole mount; False Bay, approx. 34°19'S 18°31'E; 58–62 m; 28 September 1898.

SAM–H32 (PF station 18232). Fertile colony epizootic on *Eudendrium ?deciduum* Millard; False Bay, approx. 34°27'S 18°45'E; 110 m; 11 November 1903.

Collected by: R.S. Pieter Faure.

SAM–H101 (UCT FB 119L plus FAL 289B). Male and infertile colonies epizootic on *Salacia articulata* (Pallas); plus two whole mounts; False Bay, 34°08,5'S 18°34,5'E; 27 m; 21 April 1947; and another locality in False Bay, exact location and collector unknown; 40 m; September 1897.

Collected by: University of Cape Town.

SAM–H102 (UCT FAL 26L). Infertile colony on empty tubes; one whole mount only; False Bay, 34°13'S 18°29'E; 15–21 m; 5 March 1952.

Collected by: J. C. Morgans.

Campanularia pecten Gow & Millard, 1975: 1, fig. 1.

Holotype: SAM–H1659. Male colony growing on sea-grass *Caulerpa filiformis* (Suhr); plus four whole mounts.

Locality: St James, False Bay; littoral; 29 March 1968.

Collected by: C. Gow.

Campanularia roberti Gow & Millard, 1975: 3, fig. 2.

Holotype: SAM–H1660. Female colony growing on weed *Sargassum longifolium* (Turner) attached to the kelp *Ecklonia maxima* (Osbeck); plus four whole mounts.

Locality: Partridge Point, False Bay; 24 March 1968.

Collected by: R. W. Day.

Campanularia subantarctica Millard, 1971: 403, fig. 5.

Holotype: SAM-H2920. Two whole mounts only of fertile colony epizootic on *Symplectoscyphus marionensis* Millard.

Locality: Near mouth of Soft Plume River, Marion Island; littoral; 7 February 1965.

Collected by: N. R. Fuller.

Clytia latithecata Millard & Bouillon, 1973: 55, fig. 7H-L.

Schizoholotype: SAM-H2921 (MT 2666). Two whole mounts only of fertile colony.

Locality: Praslin Island, Seychelles; 1966.

Collected by: J. Bouillon.

Clytia serrata Millard, 1958: 173, fig. 3C, H.

= *Clytia gravieri* (Billard): Millard & Bouillon, 1973: 51, fig. 7E-G.

Holotype: SAM-H115 (UCT MOR 216C). One whole mount only of infertile colony epizootic on *Eudendrium carneum* Clarke.

Locality: On wreck at Linga Linga, Morrumbene estuary, Mozambique; 15 July 1954.

Collected by: University of Cape Town.

Family Syntheciidae

Hincksella corrugata Millard, 1958: 181, fig. 5.

Holotype: SAM-H85 (PF station 12456). Infertile colony on weed; plus one whole mount.

Locality: off Natal, approx. 30°32'S 30°38,5'E; 46 m; 22 March 1901.

Collected by: R.S. Pieter Faure.

Hincksella indiana Millard, 1967: 178, fig. 3D-G.

Holotype: SAM-H1646 (UCT AFR 1235A). One infertile stem in three parts; plus one whole mount of hydrocladia.

Locality: south of Madagascar, 27°48'S 47°19'E; 875 m; 22 June 1961.

Collected by: R.V. *Africana II*.

Synthecium hians Millard, 1957: 204, fig. 9A-C.

Holotype: SAM-H107 (UCT FAL 214G). Several infertile stems; plus two whole mounts.

Locality: False Bay, 34°12,4'S 18°43,5'E; 42 m; 10 September 1953.

Collected by: University of Cape Town.

Family **Sertulariidae**

Salacia disjuncta Millard, 1964: 31, fig. 10A–F.

Holotype: SAM–H412 (UCT SCD 37K). One whole mount only (infertile).

Locality: Agulhas Bank, 32°15,2'S 28°57,7'E; 50 m; 19 May 1958.

Paratype: SAM–H1782 (UCT SCD 296H). One whole mount only (infertile); Agulhas Bank, 33°09'S 28°02'E; 84 m; 6 February 1962.

Collected by: University of Cape Town.

Sertularella agulhensis Millard, 1964: 35, fig. 12A.

Holotype: SAM–H413 (UCT TRA 151F). Several infertile stems; plus one whole mount.

Locality: Agulhas Bank, 34°51'S 19°55'E; 22 m; 6 March 1958.

Collected by: commercial trawler.

Sertularella capensis Millard, 1957: 210, fig. 10H.

Holotype: SAM–H108 (UCT FB 114A). A rich infertile colony; plus one whole mount.

Locality: False Bay, 34°07,5'S 18°31'E; 27–28 m; 22 February 1947.

Paratypes: SAM–H109 (UCT FB 115D). A fairly rich infertile colony; False Bay, 34°08'S 18°31,5'E; 27–28 m; 22 February 1947.

SAM–H110 (UCT FAL 64L). A fairly rich infertile colony; plus one whole mount; False Bay, 34°17,3'S 18°48,7'E; 37–38 m; 29 July 1952.

Collected by: University of Cape Town.

Sertularella capensis delicata Millard, 1964: 38, fig. 12B–D.

Since incorporated in *Sertularella annulaventricosa* Mulder & Trebilcock, 1915.

Holotype: SAM–H414 (UCT NAD 22F). Several infertile stems; plus one whole mount.

Locality: off Natal, 29°58'S 31°02'E; 49 m; 12 August 1958.

Collected by: University of Cape Town.

Sertularella congregata Millard, 1964: 39, fig. 13A–D.

Holotype: SAM–H415 (UCT SCD 254Q). Fertile colony; plus one whole mount.

Locality: Agulhas Bank, 33°07,3'S 28°01'E; 88 m; 16 July 1961.

Collected by: University of Cape Town.

Paratype: SAM–H185. Infertile colony; plus one whole mount; Agulhas Bank, 33°09'S 28°03'E; 86 m; 28 December 1898.

Collector unknown.

Sertularella dubia, var. *magna* Millard, 1958: 189, fig. 7A.

= *Sertularella dubia magna* Millard.

Holotype: SAM-H54 (PF station 12028). Several infertile stems; plus one whole mount.

Locality: off Natal, approx. 28°41'S 32°22'E; 62 m; 27 February 1901.

Collected by: R.S. Pieter Faure.

Sertularella falsa Millard, 1957: 211, figs 10F, 11D.

= *Sertularella polyzonias falsa* Millard.

Holotype: SAM-H111 (UCT FB 119C). A fairly rich fertile colony; plus one whole mount.

Locality: False Bay, 34°08,5'S 18°34,5'E; 27 m; 21 April 1947.

Paratypes: SAM-H112 (UCT FB 131H). Rich fertile colonies from several localities in False Bay and on various dates; plus one whole mount.

SAM-H113 (UCT CP 333B). Fertile colony; plus one whole mount; Dalebrook, False Bay; littoral; 25 August 1949.

Collected by: University of Cape Town.

Sertularella gilchristi Millard, 1964: 44, fig. 12E, G-H.

Holotype: SAM-H416 (UCT SCD 85J). A fairly rich male colony; plus one whole mount.

Locality: Agulhas Bank, 33°03'S 27°55'E; 27 m; 17 July 1959.

Collected by: University of Cape Town.

Sertularella mediterranea var. *asymmetrica* Millard, 1958: 191, fig. 7B.

= *Sertularella mediterranea asymmetrica* Millard.

Holotype: SAM-H116 (UCT IN 49K). Several female stems; plus two whole mounts.

Locality: Inhaca Island, Mozambique; littoral; 1954.

Collected by: University of the Witwatersrand.

Sertularella natalensis Millard, 1968: 271, fig. 4E-G.

Schizoholotype: SAM-H2922 (TME 23M). One whole mount only.

Locality: off Natal, 29°47,5'S 31°11,8'E; 64 m; 22 August 1929.

Collected by: Th. Mortensen's Java-South Africa Expedition.

Sertularia linealis var. *longa* Millard, 1958: 197, fig. 8E.

= *Sertularia longa*: Millard & Bouillon, 1974: 33, fig. 7D, J.

Holotype: SAM-H117 (UCT IN 140E). Infertile colony on weed; plus one whole mount.

Locality: East Shore Rocks, Inhaca Island, Mozambique; 20 July 1956.

Collected by: University of the Witwatersrand.

Symplectoscyphus marionensis Millard, 1971: 405, fig. 7.

Holotype: SAM-H2923. One whole mount only of fertile colony.

Locality: near Soft Plume River, Marion Island; littoral; 1965.

Collected by: N. R. Fuller.

Uniscyphus fragilis Millard, 1977b: 122, fig. 7E-G.

Holotype: SAM-H1982 (SM station 43). Two hydrothecae; plus one whole mount of three hydrothecae.

Locality: off Natal, 28°45,5'S 32°24,5'E; 360-420 m; 29 May 1975.

Collected by: R.V. Meiring Naude.

This is the type species of the genus *Uniscyphus* Millard, 1977.

Family Plumulariidae

Subfamily Halopterinae

Corhiza bellicosa Millard, 1962: 275, fig. 2A-E.

Holotype: SAM-H364 (UCT SCD 84S). Several infertile stems; plus one whole mount.

Locality: Agulhas Bank, 33°03'S 27°55'E; 27 m; 17 July 1959.

Paratype: SAM-H1947 (UCT SCD 153J). One infertile stem; plus one whole mount; Agulhas Bank, 34°03'S 25°59'E; 84 m; 25 November 1960.

Collected by: University of Cape Town.

Corhiza mortenseni Millard, 1968: 274, fig. 5A-D.

Schizoholotype: SAM-H2914 (TME 24). Two whole mounts only.

Locality: off Natal, 29°48,5'S 31°18'E; approx. 219 m; 22 August 1929.

Collected by: Th. Mortensen's Java-South Africa Expedition.

Corhiza pannosa Millard, 1962: 278, fig. 3A-B, D-G.

Holotype: SAM-H362 (UCT SCD 5H). One infertile colony; plus one whole mount.

Locality: Agulhas Bank, 34°15'S 25°05'E; 11 m; 19 April 1958.

Collected by: University of Cape Town.

Gattya tropicalis Millard & Bouillon, 1973: 79, fig. 10A-D.

Schizoholotype: SAM-H2924 (MT 2667). One whole mount only.

Locality: Beau Vallon, Mahé Island, Seychelles; 1966.

Collected by: J. Bouillon.

Halopteris gemellipara Millard, 1962: 282, fig. 4A–F.

Holotype: SAM–H308 (PF station 13810). An infertile colony; plus one whole mount.

Locality: Agulhas Bank, approx. 33°54'S 26°51'E; 120 m; 10 September 1901.

Collected by: R.S. Pieter Faure.

Halopteris pseudoconstricta Millard, 1975: 355, fig. 114D–G.

As *Halopteris constricta*: Millard, 1957: 227, fig. 14A.

Holotype: SAM–H542 (UCT CP 740D). Numerous pinnate stems bearing female gonophores and a few infertile simple stems; plus one whole mount.

Locality: Melkbosstrand, Table Bay; littoral; 17 November 1967.

Collected by: University of Cape Town.

Halopteris rostrata Millard, 1975: 357, fig. 114A–C.

Holotype: SAM–H543 (UCT NAD 89H). Eleven infertile stems and several damaged ones growing on skeleton of antipatharian; plus two whole mounts.

Locality: off Natal, 29°11'S 32°02'E; 70 m; 30 July 1964.

Collected by: University of Cape Town.

Monostaechas faurei Millard, 1958: 204, fig. 11.

Holotype: SAM–H58 (PF station 12028). Six male stems; plus two whole mounts.

Locality: off Natal, approx. 28°41'S 32°22'E; 62 m; 27 February 1901.

Collected by: R.S. Pieter Faure.

Monostaechas natalensis Millard, 1958: 206, fig. 12.

Holotype: SAM–H79 (PF station 12456). Many stems, male and female; plus two whole mounts.

Locality: off Natal, approx. 30°32'S 30°38,5'E; 46 m; 22 March 1901.

Paratypes: SAM–H48 (PF station 11803). One infertile stem; plus one whole mount; off Natal, approx. 29°00'S 31°49'E; 24 m; 8 February 1901.

SAM–H76 (PF station 12392). Several infertile stems; plus one whole mount; off Natal, approx. 31°02,5'S 30°18'E; 46 m; 14 March 1901.

Collected by: R.S. Pieter Faure.

Subfamily **Plumulariinae**

Plumularia antonbruuni Millard, 1967: 185, fig. 5.

Holotype: SAM-H1647 (UCT ABD 14C). Three male stems; plus one whole mount.

Locality: off Natal, 29°45'S 31°40'E; 440 m; 8 September 1964.

Collected by: R.V. *Anton Bruun*.

Plumularia irregularis Millard, 1958: 210, fig. 13A-C.

= *Kirchenpaueria irregularis*: Millard, 1975: 370, fig. 118D-G (transferred to subfamily Kirchenpaueriinae).

Holotype: SAM-H119 (UCT DBN 70Q). Three infertile stems; plus one whole mount.

Locality: Salisbury Island, Durban Bay; littoral; 22 July 1950.

Collected by: University of Cape Town.

Plumularia mossambicae Millard, 1975: 393, fig. 123E-G.

Holotype: SAM-H1866 (UCT PED 4V). One whole mount only (infertile stem).

Locality: off Mozambique, 24°46'S 35°18'E; 110 m; 18 August 1964.

Collected by: University of Cape Town.

Plumularia pennycuikae Millard & Bouillon, 1973: 85, fig. 10N-P.

As *Plumularia* sp.: Pennycuik, 1959: 183, pl. 3 (fig. 7).

Schizoholotype: SAM-H2925 (MT 2668). One whole mount only.

Locality: Silhouette Island, Seychelles; 1966.

Collected by: J. Bouillon.

Subfamily **Aglaopheniinae**

Cladocarpus crepidatus Millard, 1975: 417, fig. 130A-C.

Holotype: SAM-H537 (UCT SST 6GG). One female stem; plus one whole mount.

Locality: Agulhas Bank, 35°22'S 22°31'E; 200 m; 20 June 1972.

Collected by: University of Cape Town.

Cladocarpus natalensis Millard, 1977b: 127, fig. 10.

Holotype: SAM-H2861 (SM station 86). Five fertile stems; plus one whole mount.

Locality: off Natal, 27°59,5'S 32°40,8'E; 550 m; 22 May 1976.

Collected by: R.V. *Meiring Naude*.

Cladocarpus paries Millard, 1975: 483, fig. 143.

Holotype: SAM-H1914. One infertile stem; plus two whole mounts.

Locality: Agulhas Bank, 33°25'S 27°29'E; 70 m; 23 January 1975.

Collected by: South African Museum.

Cladocarpus unicornus Millard, 1975: 429, fig. 133E-F.

Holotype: SAM-H538 (UCT PED 4S). One infertile stem; plus one whole mount.

Locality: off Mozambique, 24°46'S 35°18'E; 110 m; 18 August 1964.

Collected by: University of Cape Town.

Halicornaria africana Millard, 1958: 215, fig. 15A-C.

= *Gymnangium africanum* (Millard).

Holotype: SAM-H120 (UCT AFR 1028B). One infertile colony; plus one whole mount.

Locality: off Natal, 28°28'S 32°25,8'E; 27 m; 15 May 1948.

Collected by: R.V. *Africana II*.

Halicornaria arcuata var. *epizootica* Millard, 1958: 218, fig. 15F.

= *Gymnangium arcuatum* (Lamouroux, 1816), epizootic form.

Holotype: SAM-H73 (PF station 12392). One whole mount only, infertile, epizootic on *Thecocarpus formosus* (Busk).

Locality: off Natal, approx. 31°02,5'S 30°18'E; 46 m; 14 March 1901.

Collected by: R.S. Pieter Faure.

Halicornaria exserta Millard, 1962: 309, fig. 11A-E.

= *Gymnangium exsertum* (Millard).

Holotype: SAM-H169 (PF station 596). One fertile stem; plus one whole mount.

Locality: Agulhas Bank, approx. 33°49'S 25°56'E; depth unknown; 11 November 1898.

Collected by: R.S. Pieter Faure.

Halicornaria exserta epizootica Millard, 1962: 309, fig. 11F-H.

= *Gymnangium exsertum* (Millard), epizootic form.

Holotype: SAM-H320 (PF station 13915). Colony epizootic on *Thecocarpus flexuosus umbellatus* Millard; plus one whole mount.

Locality: Agulhas Bank, approx. 34°05'S 26°34'E; 115 m; 23 September 1901.

Collected by: R.S. Pieter Faure.

Thecocarpus flexuosus umbellatus Millard, 1962: 316, fig. 12B, M.

Holotype: SAM-H363 (UCT SCD 36M). Large infertile colony; plus one whole mount.

Locality: Agulhas Bank, 32°15,2'S 28°57,7'E; 49,5 m; 19 May 1958.

Collected by: University of Cape Town.

Thecocarpus giardi var. *solidus* Millard, 1958: 222, fig. 16B-C.

= *Thecocarpus flexuosus solidus* Millard.

Holotype: SAM-H121 (UCT AFR 1028A). Large fertile colony; plus two whole mounts.

Locality: off Natal, 28°28'S 32°25,8'E; 27 m; 15 May 1948.

Collected by: R.V. *Africana II*.

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6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

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Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierti Philippi, 1861: 87.

Leda bicuspidata: Nickles, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

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In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

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e.g. '... the Figure depicting *C. namacolus* ...'; '... in *C. namacolus* (Fig. 10) ...'
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e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene
- Scientific names, but not their vernacular derivatives
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Reference to the author should be expressed in the third person

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N. A. H. MILLARD

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(continued inside back cover)

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THE UNIONACEA
(MOLLUSCA, LAMELLIBRANCHIATA)
OF SOUTH-CENTRAL AFRICA

By
C. C. APPLETON

Cape Town Kaapstad

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THE UNIONACEA (MOLLUSCA, LAMELLIBRANCHIATA)
OF SOUTH-CENTRAL AFRICA

By

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*Bilharzia Field Research Unit, South African Medical Research Council,
Nelspruit*

(With 8 figures and 1 table)

[MS. accepted 11 December 1978]

ABSTRACT

Twelve species of the Unionacea (Mollusca, Lamellibranchiata), five Unionidae and six Mutelidae and one Etheriidae, are recorded from the south-central region of Africa. Their distribution within this region, which is taken to embrace the catchments of the Kunene, Cuvelai, Okavango, Linyanti and Zambezi River systems, is updated. Attention is drawn to the paucity of ecological data relevant to the freshwater bivalves of Africa and the detailed locality notes made by several collectors are therefore included.

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INTRODUCTION

Knowledge of the Unionacea of the southern central African region embracing the Kunene, Cuvelai, Okavango and Zambezi River systems (i.e. between latitudes 9° and 21°S) has hitherto been limited, particularly with regard to the Kunene and Okavango. During the past decade, however, a considerable amount of material has been collected from these drainages and through the co-operation of a number of individuals and institutions the author has been able to examine examples of eleven of the twelve recorded unionacean species, five Unionidae, five Mutelidae and one Etheriidae, permitting an updating of knowledge on the composition and distribution of this bivalve fauna. Unfortunately no material is available from the middle and lower Zambezi, east of Lake Kariba. However, the bivalve fauna of Lake MacIlwaine on the Hunyani River, a tributary to the middle Zambezi, has been discussed by Marshall (1975) and the malacofauna of Lake Malawi has been dealt with by Crowley *et al.* (1964) and Mandahl-Barth (1972). In addition, the bivalves of the adjacent Bangweulu-Luapala basin, the Congo River system, and Mozambique have been variously discussed by Mandahl-Barth (1968), Pilsbry &

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Bequaert (1927), Azevedo *et al.* (1961), and Braga (1952). In the present contribution the systematic arrangement of Connolly (1939) has been followed, though changes in nomenclature made by Haas (1969), Mandahl-Barth (1968, 1972) and Heard & Vail (1976) have been incorporated.

Figure 1 shows the watercourses referred to in the text. These comprise both large, perennial rivers such as the Kunene and Okavango with volumes that may exceed 6 000 m³/s during high flood which can drop to less than 15 m³/s in dry years (Stengel 1963), as well as largely seasonal floodplain or deltaic environments such as the Okavango delta, Linyanti swamp, eastern Caprivi floodplain and the Etosha Pan.

Where measurements of shell height (altitude) are given, maximum height is used (except where indicated) in preference to umbonal height because in many cases the umbones were eroded to such an extent that considerable inaccuracies would have been introduced.

The following abbreviations are used:

SAM	South African Museum, Cape Town
NM	Natal Museum, Pietermaritzburg
TM	Transvaal Museum, Pretoria
MMK	McGregor Memorial Museum, Kimberley
SMN	State Museum, Windhoek

Where no abbreviations are given, the material has been lodged in the collection of the South African Museum, Cape Town.

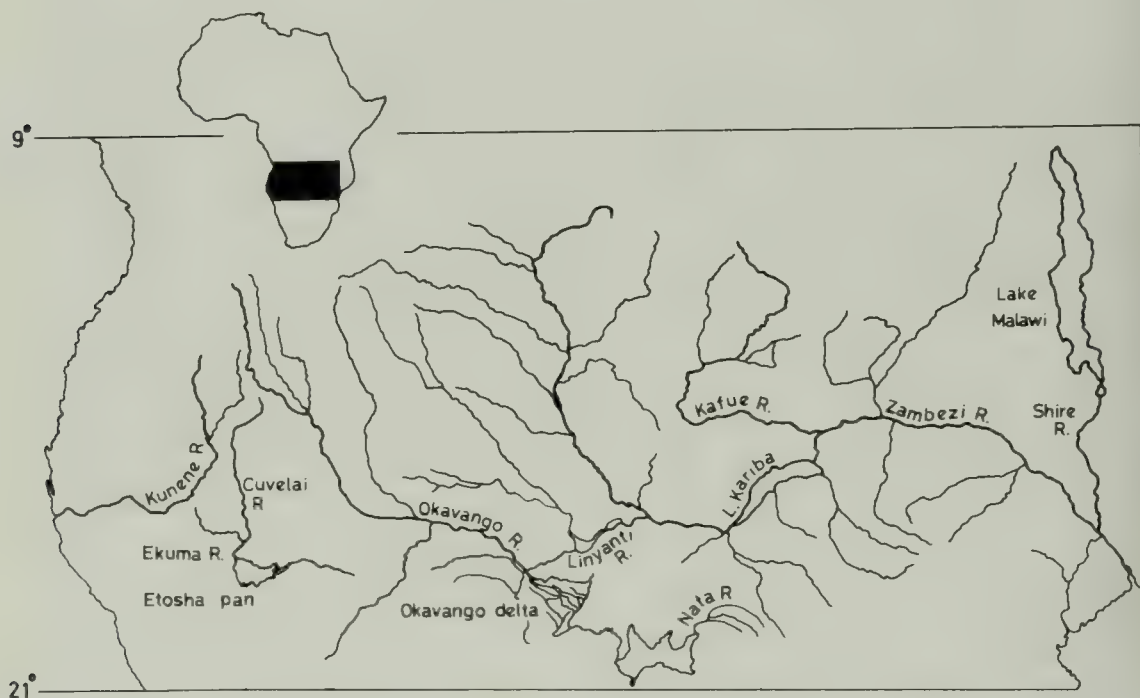


Fig. 1. Map of south-central Africa (between latitudes 9° and 21°S) showing the river systems referred to in the text.

SYSTEMATIC DISCUSSION

Superfamily UNIONACEA

Family Unionidae

Although many species of Unionidae have been described from southern Africa (south of but including the investigated area) only four are recognized here. These are *Unio caffer*, *Caelatura kunenensis*, *C. mossambicensis* and *C. framesi* and may even be too many. All except *C. framesi*, a southerly species, occur in the area under discussion.

Unio Retzius, 1788

Unio caffer Krauss, 1848

Fig. 2A

Material examined

Zambezi River system:

Kafue River south of Itezehitshi, Zambia. R. M. Derricourt leg. 1975,
2 specimens + 1 valve.

Matopos, Rhodesia, M. N. Bruton leg. 1973, 3 specimens.

Nyamandelelovu (on Gwaai River), Rhodesia. R. H. R. Stevenson leg.
26 May 1924, 1 specimen, NM-A5364.

Victoria Falls, collector unknown, 1 valve, MMK MOL-328.

Upper Zambezi River, G. C. Shortridge leg., 1 valve, MMK MOL-327.

Hunyani River, Darwendale, B. E. Marshall leg. May 1975, 2 specimens
+ 1 valve.

Gwenoro dam, Gwelo, Rhodesia. B. E. Marshall leg., 1 specimen.

Heard & Vail (1976) have discussed in detail the anatomy and systematic position of this species and have illustrated its hooked glochidium. These glochidia are considerably smaller than those of *Caelatura kunenensis* found by the present author. *Unio caffer*, which attains a far larger size than any other southern African unionid, is characterized by its heavy shell, strong cardinal and lateral teeth and downward-sloping hinge line. The posterodorsal ridge is usually pronounced though not sharp. Some zigzag sculpture is present on juvenile shells up to about 21 mm in length; on older shells this is generally worn away and only growth striae remain. Only the outer demibranchs are modified to form marsupia.

The records from the Kafue and upper Zambezi rivers are the most northerly for this southern African species. Marshall (1975) has reported it from Lake MacIlwaine (Rhodesia). It is, however, uncommon in the area under discussion and has not been recorded from the Okavango, Cuvelai or Kunene River systems, i.e. west of longitude 23°E.

A record of *U. caffer* from Amaramba in the Niassa district of Mozambique (Azevedo *et al.* 1961), consisting of a single juvenile approximately

6,1 × 3,6 × 2,2 mm, has been suggested by Oberholzer & Van Eeden (1967) to refer to a higher-shelled species, viz. *Caelatura mossambicensis*. This is probably correct since the Amaramba specimen has a L/H ratio of 1,70 whereas a juvenile *U. caffer* of similar size from the eastern Transvaal escarpment has a ratio of 1,95. No juvenile *C. mossambicensis* are available but comparable *C. kunenensis* from the Kafue River (NM-A5366) have L/H ratios of 1,58–1,62. Furthermore, the illustration by Azevedo *et al.* (1961) of sculpture round only the umbone is in agreement with the general paucity of sculpture found in *C. mossambicensis* and is in marked contrast to juvenile *U. caffer* where a sculpture pattern of two to three broken chevrons crosses the entire shell.

Unio is a palearctic genus whose distribution in Africa is, as Brown (1978) has pointed out, restricted to the cooler regions of the continent. There is thus a wide gap between the ranges of *U. caffer* in South Africa, South West Africa and Rhodesia and that of the nearest related species in North Africa.

Caelatura Conrad, 1853

Caelatura kunenensis (Mousson, 1887)

Fig. 2B–C

Material examined

Kunene River system:

Pump station, Huila (district), Angola, M. J. Penrith & J. Batista leg. 29 September 1972, 2 specimens, SMN-75540.

Pool below Ruacana Falls, B. F. Kensley leg. 1972, 50 specimens + 11 valves.

Ruacana Falls (17°23'S, 14°13'E), M.-L. Penrith leg. 1976, 10 specimens, SMN-75598.

Great (Kambe) Falls (according to M. J. Penrith this is probably an old name for the minor cataracts about 10 km above Ruacana), K. H. Barnard leg. 1923, 2 valves, SAM-A6640 and A6647.

44 km west of Ondarusu Falls, M. J. Penrith leg. 23–25 October 1971, 1 specimen, SMN-75494.

72 km west of Ondarusu Falls, M. J. Penrith leg. 28 October 1971, 1 specimen, SMN-75494.

Kunene River at Otjinungua, W. D. Haacke leg. May 1966, 2 specimens, TM-9334 and 9335.

Cuvelai/Etoshia system:

Ekuma floodplain, Etoshia Pan National Park, K. L. Tinley leg. 27 December 1965, 1 specimen, NM-A5369.

Okavango River system:

Okavango River, G. C. Shortridge leg., 5 specimens, NM-3999; 3 specimens, TM-38541.

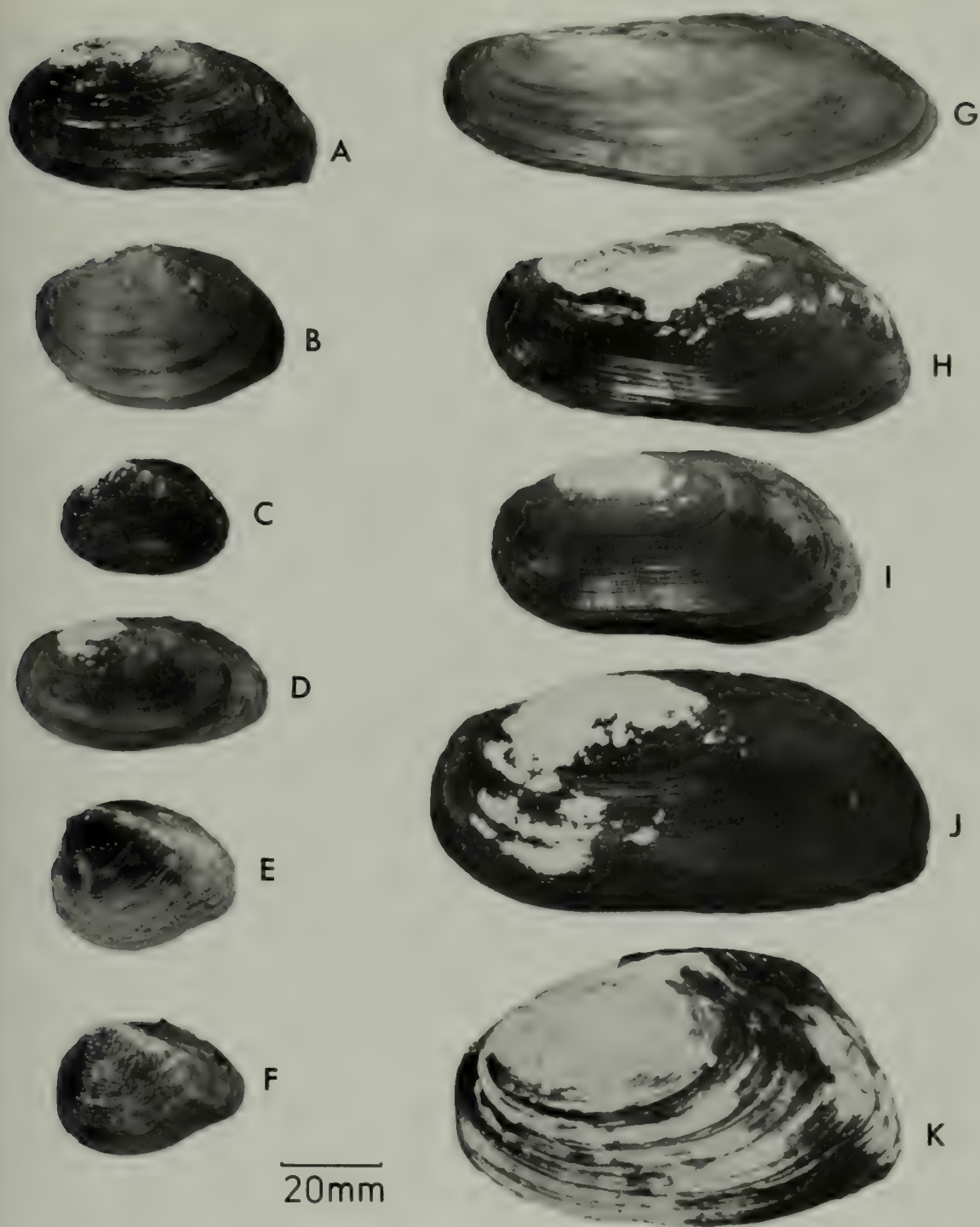


Fig. 2. Left valves of ten species of Unionacea from south-central Africa.

- A. *Unio caffer* Krauss, 1848, Kafue River south of Itezihitezhi, Zambia. 62,5 × 31,9 mm.
 B. *Caelatura kunenensis* (Mousson, 1887), 'typical form', Thamalakane River in Okavango delta, Botswana. 50,2 × 33,2 mm. C. *Caelatura kunenensis* (Mousson, 1887), 'Zambezi form', Kalala Island in Kafue River, Zambia. 33,8 × 23,4 mm. D. *Caelatura mossambicensis* (Martens, 1859), eastern end of Lake Kariba, Rhodesia. 50,8 × 27,0 mm. E. *Caelatura nyassaensis* (Lea, 1964), off Nkopola, Lake Malawi, Malawi. 37,6 × 31,0 mm. F. *Caelatura hypsiprymna* (von Martens, 1897), off Nkopola, Lake Malawi, Malawi. 37,3 × 28,3 mm. G. *Mutela dubia* (Gmelin, 1793). Thamalakane River in Okavango delta, Botswana. 101,3 × 36,1 mm. H. *Mutela alata* (Lea, 1864). Lake Malawi, 87,7 × 41,0 mm. I. *Aspatharia* (*Aspatharia*) *pfeifferiana* (Bernardi, 1860), upper Zambezi River, Zambia. 78,3 × 38,0 mm. J. *Aspatharia* (*Spathopsis*) *wahlbergi* (Krauss, 1848), eastern end of Lake Kariba, Rhodesia. 102,5 × 49,2 mm. K. *Aspatharia* (*Spathopsis*) *nyassaensis* (Lea, 1864), Lake Malawi, Malawi. 91,5 × 56,4 mm.

Omuramba Omataka, G. C. Shortridge leg., 22 specimens, MMK MOL-327. Label reads: 'everything collected in dry annually flooded bed of Omuramba Omataka at or within 15 miles (23 km) of junction with Okavango'. (The Omuramba Omataka is the largest, albeit seasonal, watercourse flowing from South West Africa to the Okavango River.)

Thamalakane River at Maun, Okavango delta, collector unknown, 20 May 1930, 181 specimens + 14 valves, TM-5565; same locality, P. A. Reavell leg. 1973, 147 specimens.

Rakops on the Botletle River between the Okavango delta and the Makarikari Pan, collector unknown, 3 specimens.

Chobe/Linyanti River system:

Luapala Island in Linyanti swamp, 17°22'S 23°42'E 'from shallow sand-bank, water level dropped'. B. van der Waal leg. 1975, 1 specimen + 2 valves.

Zambezi River system:

'Zambezi', 1 specimen + 1 valve, NM-3371.

'Zambezi', B. E. Marshall don., 4 specimens.

Zambezi at Mongu Lealui, Barotse Valley, Zambia, 5 specimens + 1 valve, NM-4000. Type locality of *Nodularia croninae*, synonym of *C. kunenensis*.

Upper Zambezi River, G. C. Shortridge leg., 2 specimens + 21 valves, MMK MOL-327.

Zambezi at Katima Mulilo, eastern Caprivi, W. D. Haacke leg. May 1966, TM-11009; same locality, B. van der Waal leg. 1975, 3 specimens; R. J. Pitchford leg. 1976, 2 valves.

Victoria Falls, K. H. Barnard leg. 1946, 2 specimens + 1 valve.

Kafue River, Kalala Island Rest Camp, Kafue National Park, Zambia, A. C. van Bruggen leg. 2-3 November 1966, 3 specimens + 8 valves, 'ex flood debris of Kafue River', NM-A5366.

Kalala Island in Kafue River, Zambia, R. M. Derricourt leg. 1975, 26 specimens + 8 valves.

Itezhezhi area of Kafue River, Zambia, R. M. Derricourt leg. 1975, 10 specimens + 5 valves.

Although Haas (1936, 1969) included *Unio zambeziensis* Preston and *Nodularia croninae* Walker from the Zambezi River system in the synonymy of this species, two distinct forms are nevertheless recognizable, at least in adult shells. A generally small, robust form, dark brown in colour and usually with zigzag sculpture over most of the shell, corresponding to *Unio zambeziensis* (hereafter referred to as the Zambezi form) from the Victoria Falls is also known from the northern tributaries of the Zambezi as well as the Kunene River. A larger though more compressed form, with a lower length/height ratio, light brown

in the adult stage and with sculpture over much of the shell, occurs in the Okavango River and its delta, and in the Linyanti swamp. This latter form, according to Mandahl-Barth (*in litt.* 13 October 1976), corresponds to typical *C. kunenensis*. An apparently intermediate form occurs in the Zambezi River at Katima Mulilo, the Okavango River and Ekuma floodplain. Shells referable to *Nodularia croninae* are known from the upper reaches of the Zambezi in eastern Zambia. Figure 3 shows a significant difference ($p < 0.01$) between the shapes (as indicated by L/H v. length) of the Zambezi form and typical *C. kunenensis*, particularly amongst larger specimens. There is no meaningful difference in shell width relative to length and these dimensions are not shown. The measurements given by Darteville (1939) for five specimens of *C. kunenensis* from the upper Kunene (no precise locality given) indicate that these should belong to the typical form.

Juveniles up to approximately 34×23 mm may be sculptured over the whole shell surface. In larger shells the sculpturing persists posteriorly and anteriorly, although specimens corresponding to *N. croninae* are generally smoother than the more southerly forms. Juveniles of the Zambezi form are usually green-yellow. The very small valves from the Kafue River (NM-A5366) are dominated by rugose and sometimes lamellate zigzag sculpture over the whole shell surface.

Nothing is known of the nature of the localities where shells corresponding to *N. croninae* were found, but the Zambezi form and typical *C. kunenensis* may represent adaptations to fundamentally different environmental conditions. The present data indicate that the former occurs in lotic environments (perennial, flowing rivers) whereas the latter is found in lentic and often seasonally inundated areas. G. Mandahl-Barth has suggested (*in litt.* 13 October 1976) that the Zambezi form may, in fact, be a subspecies of *C. kunenensis*. *Caelatura*

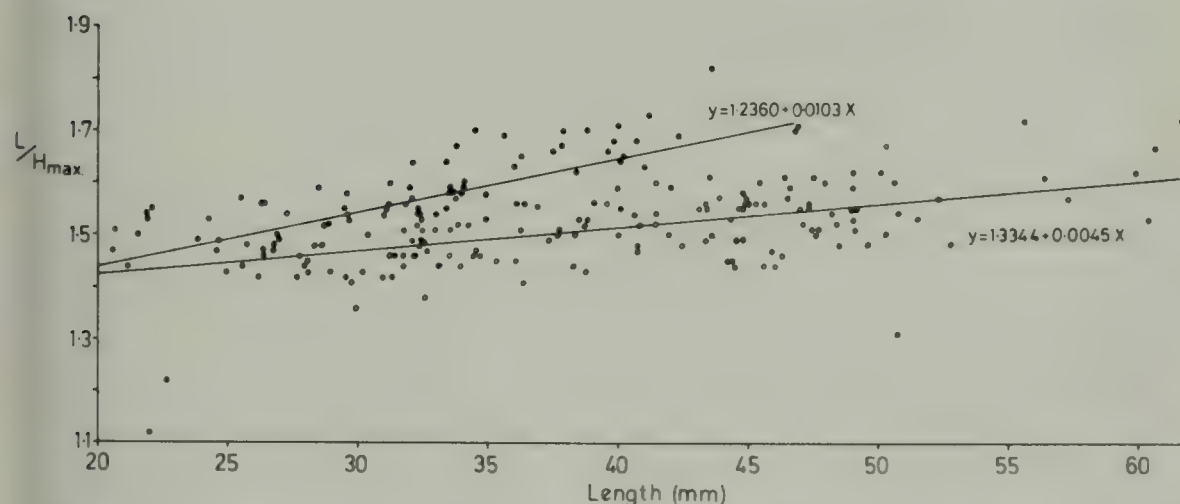


Fig. 3. *Caelatura kunenensis*: relationship between L/H and length of river (Ruacana Falls, Kunene River, $n = 71$) and swamp (Thamalakane River, Okavango delta, $n = 145$) forms as shown by linear regression lines fitted by the method of least squares. Solid circles = Kunene River; open circles = Okavango delta.

kunenensis is thus a western species confined to the Kunene and Okavango River systems as well as the upper Zambezi and its tributaries (Kafue, Luapala and Linyanti) as far north as approximately 11°S latitude. The 'typical' form seems allied to *Caelatura choziensis* (Preston) from Lake Bangweulu and the Chambeshi River as illustrated by Haas (1936) and Mandahl-Barth (1972).

Although the gonads were not examined histologically, dissection of a series of specimens from below the Ruacana Falls in the Kunene River showed that 58 per cent (25/43) were functional females with all four demibranchs modified to marsupia. The remaining 42 per cent (18/43) bore no sign of marsupia and were considered males. The smallest female measured $25,6 \times 17,8 \times 12,0$ mm. Although most marsupia were charged with embryos some contained sub-oval glochidia. The uniformly punctate valves of these glochidia were virtually equal in length and height (Fig. 4); the mean dimensions of six examples were $0,263 \times 0,265$ mm. No hooks were seen, although the glochidia may not have been fully developed.

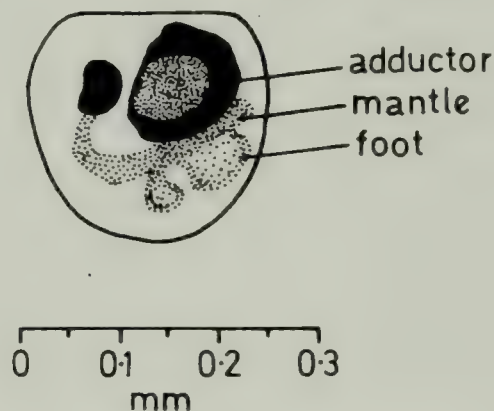


Fig. 4. Camera lucida drawing of a glochidium from an outer demibranch of *Caelatura kunenensis* ($38,6 \times 23,2 \times 17,6$ mm) from Ruacana Falls, Kunene River.

Small leeches, *Batracobdella tricarinata* (Blanchard) were found in the pallial cavities of 16,3 per cent (7/43) of *Caelatura kunenensis* from Ruacana on the Kunene River and a single ephemeropteran nymph (Baetidae: *Centroptiloides*? sp.) was present in the pallial cavity of a specimen from the Zambezi at Katima Mulilo. Although this nymph is unlikely to be a 'pallial cavity' dweller, *Centroptiloides* nymphs are unusual among mayflies in being predaceous (F. M. Chutter, *in litt.* 31 January 1977). The presence of insect larvae inside bivalves was also noted by Beedham (1971) who found chironomid larvae between the mantle and shell of *Anodonta cygnea* (Linnaeus) (Unionidae) in England. Woodward (1974) recorded numerous examples of a hydracarine (though not a parasitic stage) within the pallial cavity of *Caelatura* cf. *aegyptica* (Cailliaud) from Lake Chad.

Caelatura mossambicensis (von Martens, 1860)

Fig. 2D

Material examined

Zambezi River system:

Eastern end of Lake Kariba in Nyanyana River estuary, Sanyati basin, 5–7 m in soft sand/silt, D. H. S. Kenmuir leg. 17 December 1976, 49 specimens.

Lake MacIlwaine (on Hunyani River, tributary to Zambezi), B. E. Marshall leg., 14 specimens + 14 valves.

Hunyani River at Darwendale, Rhodesia (below Lake McIlwaine), B. E. Marshall leg., 3 specimens.

This species may be distinguished from *Caelatura kunenensis* by being relatively longer and more compressed, and by having a thinner shell with poorly developed sculpture. In order to demonstrate the differences between the shell width v. length ratio of *C. mossambicensis* and *C. kunenensis*, the Lake Kariba *mossambicensis* were compared statistically to *kunenensis* from three other localities, the Kafue River, Kunene River and Okavango delta. Linear regression lines were fitted to each of the four sets of data by the method of least squares and their slopes (not shown) compared in a pairwise manner (Table 1). This showed that the shell width v. length ratio of all the *C. kunenensis* populations differed significantly from *C. mossambicensis*, whereas there was no significant difference between any of the individual *C. kunenensis* populations. The three sets of data for *C. kunenensis* were then pooled and compared with *C. mossambicensis* from Lake Kariba (Fig. 5). This showed a significant difference ($p < 0.001$) between the shell width v. length ratio for the two species.

TABLE 1

Pairwise comparisons between (A) *Caelatura mossambicensis* from Lake Kariba and (B) *C. kunenensis* from the Kafue and Kunene rivers and the Okavango delta, using the slopes of individual regression lines for shell width v. length.

A. Comparison between *C. mossambicensis* and *C. kunenensis*

<i>C. mossambicensis</i>	<i>C. kunenensis</i>	t	degrees of freedom	significance
Lake Kariba	Kafue River	2,1400	68	*
Lake Kariba	Kunene River	3,1318	108	**
Lake Kariba	Okavango delta	3,7227	191	***
Lake Kariba	three above localities combined	19,5344	279	***

B. Comparison between three geographically different populations of *C. kunenensis*

Localities		t	degrees of freedom	significance
Kafue River	Kunene River	1,0691	84	ns
Kafue River	Okavango delta	1,0069	167	ns
Kunene River	Okavango delta	0,1677	207	ns

* = significant at 5% level

** = significant at 1% level

*** = significant at 0.1% level

ns = not significant

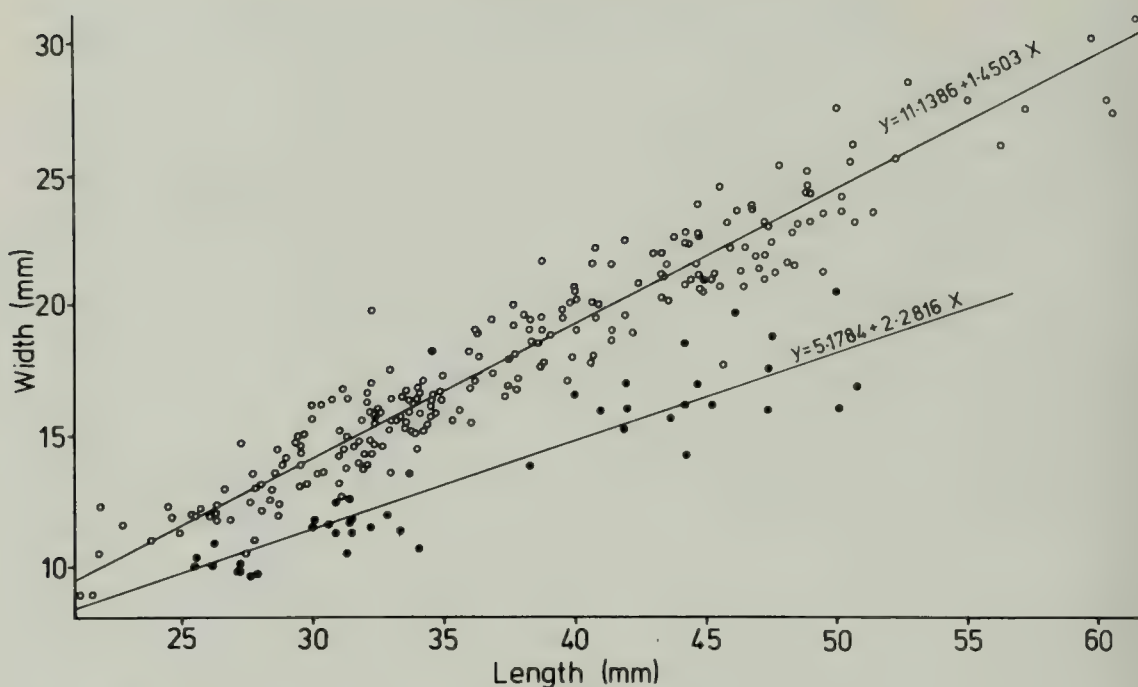


Fig. 5. Diagram relating shell width to shell length for *Caelatura kunenensis* (open circles) and *Caelatura mossambicensis* (solid circles) by means of linear regression lines fitted by the method of least squares.

Juvenile *C. mossambicensis* show zigzag sculpture anterior and posterior to the umbones, but in adults only a little remains visible. The colour of the periostracum varies from green-brown to uniform dark brown while juveniles may be light brown to greenish. Teeth are much weaker and less projecting than in *C. kunenensis*.

The type locality of *C. mossambicensis* is Tete on the lower Zambezi. It has also been recorded near Chemba (Germain 1935) and Mazarra (Azevedo *et al.* 1961; Connolly 1939) and in Lake MacIlwaine on the Hunyani River, Rhodesia (Marshall 1975). In addition, it has been collected from Lake Malawi, its tributary the South Rukuru River, and the Shire River which connects the lake to the Zambezi (Mandahl-Barth 1972). *Caelatura mossambicensis* is closely allied to *Caelatura framesi* (Connolly 1925b) from further south (Brown 1967; Appleton 1977), and Mandahl-Barth (*in litt.* 14 December 1976) is of the opinion that *C. framesi* is merely a southerly form of *C. mossambicensis*. The distribution of these two 'species' abut one another in central Mozambique. *Caelatura mossambicensis* thus appears to be an eastern species confined to the coastal peneplain of east and south-east Africa from the Kingani River near Bagamoyo in Tanzania (about 6°25'S) (Haas 1962) to the Pongola River floodplain (about 27°00'S) in north-eastern Natal (Appleton 1977; Brown 1967; Pretorius *et al.* 1975), and penetrating the Zambezi River system as far as Lakes Kariba and Malawi.

Caelatura nyassaensis (Lea, 1864)

Fig. 2E

Material examined

Monkey Bay, Lake Malawi, M. N. Bruton leg. March 1973, 1 specimen; alive in sandy mud at about 3 m, C. C. Appleton & D. H. Eccles leg. September 1976, 4 specimens.

Off Nkopola, Lake Malawi, alive in sand about 3 m, C. C. Appleton leg. September 1976, 3 specimens + 1 valve.

A small, squat shell with very little or no sculpture, ventral margin curved downward posteriorly and sharp umbonal ridge. The L/H ratio of the specimens examined ranged from 1,24 to 1,40 (mean 1,32).

Caelatura hypsiprymna (von Martens, 1897)

Fig. 2F

Material examined

Monkey Bay, Lake Malawi, B. Boswell leg., 3 specimens + 1 valve, TM-11239; alive in sandy mud at about 3 m, C. C. Appleton & D. H. Eccles leg. September 1976, 4 specimens.

Off Nkopola, Lake Malawi, alive in sand about 3 m, C. C. Appleton leg. September 1976, 8 specimens + 2 valves.

Another small, squat species with more chevron sculpture than *C. nyassaensis*. This sculpture sometimes extends over most of the shell and is particularly evident in smaller individuals which, as Mandahl-Barth (1972) has pointed out, bear a close resemblance to the Zambezi form of *C. kunenensis*. The umbonal ridge of *C. hypsiprymna* is pronounced though not sharp and the shell tends to be rather attenuated posteroventrally. The L/H ratios of those examined range from 1,13 to 1,53 (mean 1,34).

These two species appear to be endemic to Lake Malawi and have been recorded from many localities in the lake and Shire River at Mangoche to depths of 12,2 m (*C. nyassaensis*) and 79,3 m (*C. hypsiprymna*) (Crowley *et al.* 1964; Mandahl-Barth 1972). Mandahl-Barth (1972) gives a good description of the differences between these species. To this it may be added that their L/H ratios are lower than those of other Caelaturae of south-central Africa.

Family Mutelidae

Mutela Scopoli, 1777*Mutela dubia* (Gmelin, 1793)

Fig. 2G

Material examined

Kunene River system:

Pool below Ruacana Falls, B. F. Kensley leg. 1973, 4 specimens.

Okavango River system:

Okavango River, S.W.A., G. C. Shortridge leg. 5 specimens, NM-3912; 3 specimens + 1 valve, MMK MOL-336.

Thamalakane River at Maun, Okavango delta, donor unknown, 2 specimens, TM-1075; P. A. Reavell leg. 1973, 42 specimens.

Chobe/Linyanti River system:

Lupala Island in Linyanti swamp, 17°22'S 23°42'E, 'from shallow sand-bank, water level dropped'. B. van der Waal leg. 1973, 7 specimens.

Mutualutze Lusese, a large permanent channel or 'mulapo' in eastern Caprivi floodplain, 17°45'S 24°44'E. B. van der Waal leg. 1973, 1 specimen.

Zambezi River system:

Zambezi at Mongu Lealui, Barotse Valley, Zambia, Mrs. T. H. Howard leg., 1 specimen, NM-3914.

Upper Zambezi, G. C. Shortridge leg., 1 specimen, MMK MOL-336.

Zambezi at Katimo Mulilo, B. van der Waal leg. 1975, 1 specimen.

Eastern end of Lake Kariba, Nyanana estuary in Sanyati basin, 5-7 m in soft sand/silt, D. H. S. Kenmuir leg. 17 December 1976, 8 specimens.

Connolly (1939) identified *Mutela mabilli* (Rochebrune) from the Okavango River but Haas (1936), after examining the same material, recorded it as *M. nilotica mabilli*, a southern race of the north African *M. nilotica*. Later, however, Haas (1969) placed *M. mabilli* into synonymy with the west African *M. dubia*. Although the present material varies considerably in shape from almost triangular to lanceolate, the majority of shells do, in fact, correspond well to *M. dubia* as illustrated by Pilsbry & Bequaert (1927).

Both thin and thick (robust) shelled forms may occur in the same locality, but the former appears to be the most common. The thick-shelled form from the Okavango delta is on average 4.9 g heavier than the thin-shelled form of similar length, and has a rather distinct shape (Fig. 6).

Mutela dubia is a west African species which reaches the southernmost limits of its distribution in the Kunene, Okavango and Zambezi systems. The only other record of *M. dubia* from the Kunene is a brief reference to this species from the upper Kunene by Darteville (1939). The accuracy of the record of *Mutela rostrata* (Rang) (now included in the synonymy of *M. dubia* by Haas (1936, 1969)) from Lourenço Marques (Maputo) was questioned by Connolly (1925a, 1939) and to the present author's knowledge it remains the only record of *Mutela* from Mozambique south of the Zambezi River. Small leeches, *Batracobdella tricarinata* (Blanchard) (Branchiobdellidae), were found in the mantle cavities, notably around the palps, of two Ruacana (Kunene) specimens. The decimation of the littoral *M. dubia* population of Lake McIlwaine (Rhodesia) after a drop in water level (Marshall, 1975, 1978) may have been due in part at least to the natural gape of the valves of this species reducing the species' resistance to dessication.

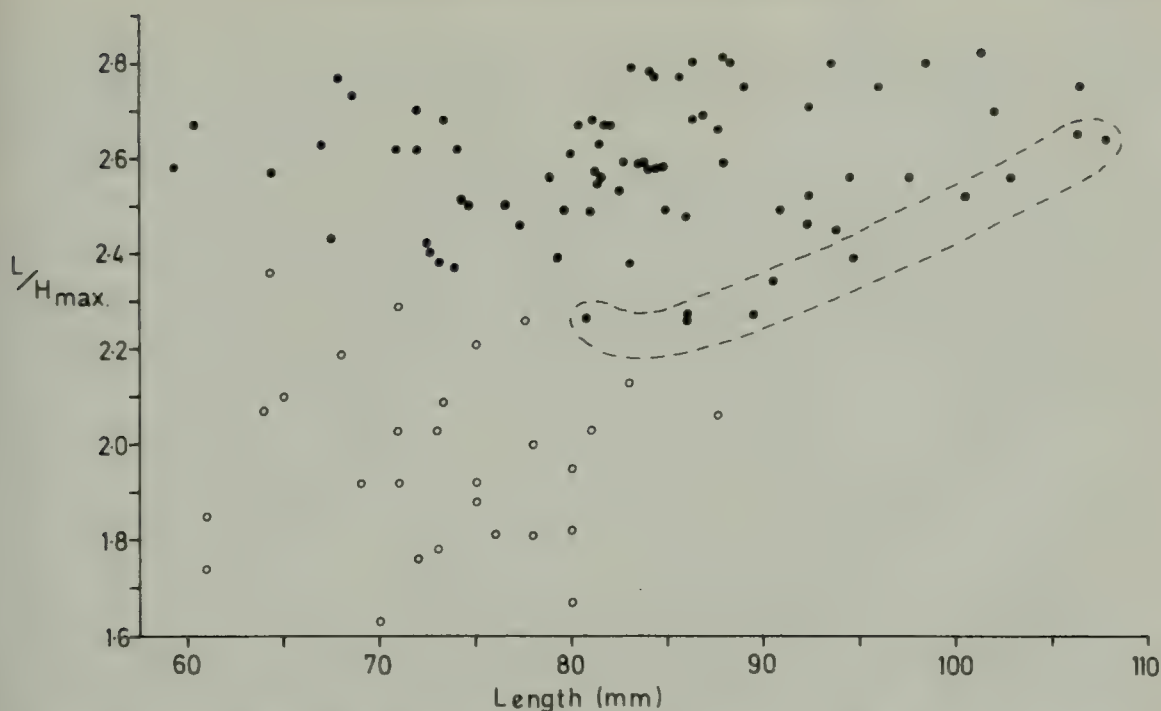


Fig. 6. *Mutela dubia*: scatter diagram relating L/H_{\max} to valve length. The dotted line indicates the robust form which constituted 22,3 per cent of *M. dubia* from the Okavango delta. Solid triangles = Zambezi River; open triangles = eastern Caprivi/Linyanti floodplain; solid circles = Okavango River system; open circles = Kunene River.

Mutela alata (Lea, 1864)

Fig. 2H

Material examined

Monkey Bay, Lake Malawi, M. N. Bruton leg. March 1973, 3 specimens;
C. C. Appleton leg. September 1976, 1 specimen.

Known from a variety of localities in Lake Malawi and the Shire River to a depth of 27,5 m (Crowley *et al.* 1964; Mandahl-Barth 1972). Both thin- and thick-shelled forms occur amongst the material available. *Mutela alata* is characterized, as its name implies, by its high (alate) posterodorsal 'wing', though this is not as high as that of *Mutela harger*i (Smith) from Lake Mweru (Zambia). The L/H ratio (2,06–2,36) tends to be lower than for *M. dubia* (2,26–2,82) (Fig. 6).

This species is apparently endemic to Lake Malawi and the Shire River although Mandahl-Barth (1972) considered that it is related to *M. harger*i and (*in litt.* 2 February 1977) to the widely distributed *dubia*–*nilotica*–*mabilli* group.

Aspatharia Bourguignat, 1885

Representatives of two subgenera, *Aspatharia* s.s. and *Spathopsis*, occur in southern central Africa and may be distinguished by the character of the inhalent opening into the branchial chamber. In *Aspatharia* s.s. there is a distinct inhalent aperture formed by a fusion of the mantle edges, while in *Aspatharia* (*Spathopsis*) there is no such fusion and the mantle margins thus

remain free below the exhalent aperture (Fig. 7). In this respect *Aspatharia* s.s. is unique among the southern and central African Unionacea.

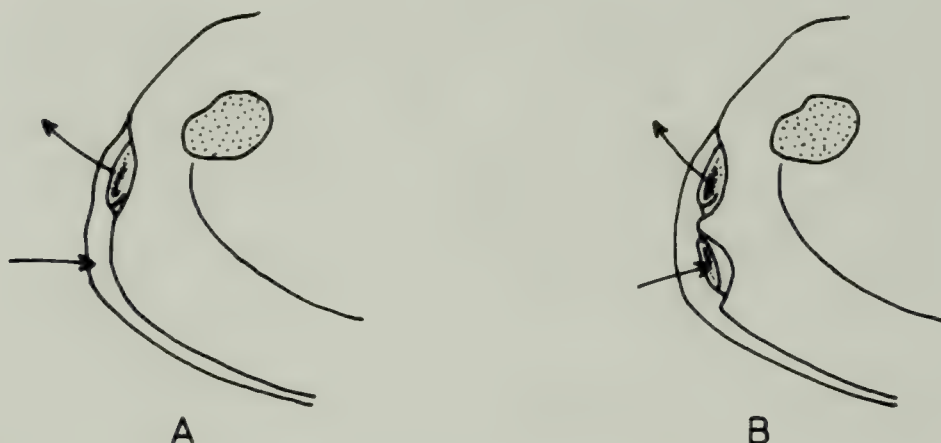


Fig. 7. Digrammatic illustration comparing the inhalent apertures of *Aspatharia* (*Aspatharia*) and *Aspatharia* (*Spathopsis*). A. *Aspatharia* s.s. lacks a discrete aperture and the inhalent current is simply drawn between the mantle edges into the branchial chamber. B. *Aspatharia* (*Spathopsis*) possesses a distinct inhalent aperture through which the current enters the branchial chamber.

Aspatharia (*Aspatharia*) *pfeifferiana* (Bernardi, 1860)

Fig. 2I

Material examined

Kunene River system:

Pool below Ruacana Falls, B. F. Kensley leg. 1973, 1 specimen.

Ontoruthu Falls (= Ondorusu Falls, 17°24'S 13°57'E), B. F. Kensley leg. 1972, 4 specimens + 2 valves.

Otjinungua, Kaokoveld, W. D. Haacke leg. May 1966, 1 specimen, TM-9335.

Okavango River system:

Okavango River, South West Africa, G. C. Shortridge leg., 6 specimens, NM-3913.

Omuramba Omataka, G. C. Shortridge leg., 7 specimens, MMK MOL-334.

Boro River, Okavango delta, P. A. Reavell leg. 1973, 3 specimens + 5 valves.

Zambezi River system:

Upper Zambezi Valley, G. C. Shortridge leg., 7 specimens, MMK MOL-334.

Sandbank in Zambezi at Katima Mulilo, B. van der Waal leg. 1974, 1 specimen.

Itezhtezhi area of Kafue River, Zambia, R. M. Derricourt leg. 1975, 1 specimen + 3 valves.

Records of this smallish species from the Kunene River at Fort Roçados in southern Angola, the Okavango River in Owambo, and the Hunyani River (a tributary of the Zambezi) in Rhodesia were cited by Haas (1936).

Aspatharia pfeifferiana is a predominantly west African species reaching the southern limits of its range in this area. In several localities it was found together with *A. (Spathopsis) wahlbergi* from which it may be distinguished by its concave ventral margin and much smaller pedal protractor muscle scar. Empty shells of *A. pfeifferiana* can usually be distinguished from those of *A. wahlbergi* as shown in Figure 8. This relates the $L/H_{\text{ad umbone}}$ ratio to

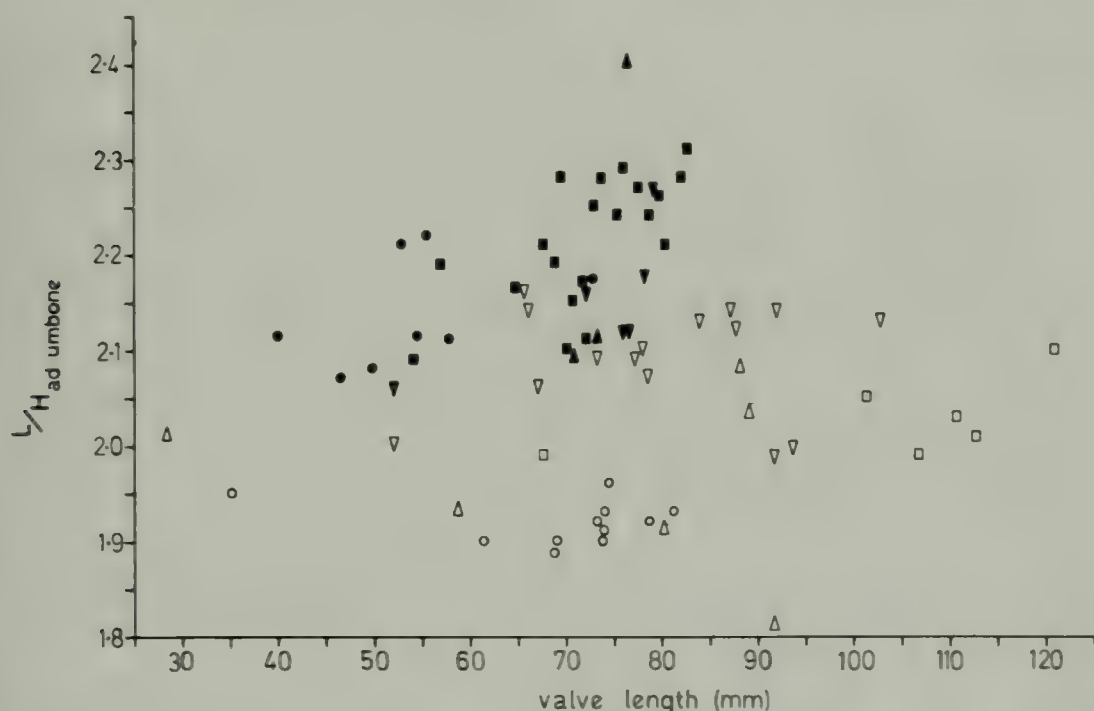


Fig. 8. Scatter diagrams relating the $L/H_{\text{ad umbone}}$ ratio to valve length for *Aspatharia (A.) pfeifferiana* (solid symbols) and *Aspatharia (S.) wahlbergi* (open symbols). Circles = Kunene River; triangles = Kafue River; inverted triangles = Zambezi River system; squares = Okavango River system.

valve length; umbonal height is used despite shell erosion in order to take into account the marked concavity of the ventral margin (below the umbonal area) typical of *A. pfeifferiana*.

The only other member of *Aspatharia* s.s. recorded from south-central Africa is *A. (A.) subreniformis* (Sowerby) from Lake Malawi and the Shire River. Mandahl-Barth (1972) doubts that this represents a valid species endemic to the lake and has suggested that it may be closely related to *A. (A.) pfeifferiana* (Bernardi) (= *A. rugifera* (Dunker) *fide* Haas 1969).

Aspatharia (Spathopsis) wahlbergi (Krauss, 1848)

Fig. 2J

Material examined

Kunene River system:

Ruacana Falls, M. L. Penrith leg. 1973, 6 specimens, SMN-75597.

Pool below Ruacana Falls, B. F. Kensley leg. 1973, 4 specimens + 1 valve.

Okavango River system:

Nata River valley, between Maitengwe and Nata Police Station, Central district Botswana, donor unknown, 3 specimens + 4 valves, TM-11237.

Zambezi River system:

Eastern end of Lake Kariba, Nyanana estuary in Sanyati basin, 5-7 m in soft sand/silt, D. H. S. Kenmuir leg. 17 December 1976, 13 specimens.

Battlefields (on Sanyati River), Rhodesia, F. B. Parkinson leg., 1 specimen, NM-2703; 1 specimen, NMK MOL-335.

Kalala Rest Camp, Kafue National Park, Zambia, 'ex flood debris of Kafue River', A. C. v. Bruggen leg. 2-3 November 1963, 1 valve, NM-A5365.

Itezihitezhi area of Kafue River, Zambia, R. M. Derricourt leg. 1975, 1 specimen + 3 valves.

Monkey Bay, Lake Malawi, B. Boswell leg. July 1968, 2 specimens, TM-11238.

Juveniles may display up to thirteen irregular riblets on the posterodorsal surface of the shell. They generally have a light-brown periostracum, but this darkens with age and adult specimens are dark brown to black. *A. wahlbergi* is also known from Mupa on the Cuvelai River, southern Angola (Haas 1936). This large species is widely distributed in central and east Africa from the Kunene River in the west to Mozambique in the east and thence southwards to the Transvaal and Zululand. Except for a single high-shelled juvenile from the confluence of Omuramba Omataka and Okavango rivers (Connolly 1931), and several specimens from the Nata River which flows into the Makarikari pan, *A. wahlbergi* has not been collected from the Okavango River system. Connolly's (1931) description of the singleton from South West Africa (L/H 1,71) is reminiscent of the Kunene River specimens whose L/H ratios (1,75-1,86, mean 1,82) are low for the species and which probably correspond to the variety *moutai* described by Dartevelle (1939) from the upper Kunene. The Nata River shells are much larger (to 120,9 × 62,1 mm, mean L/H 1,91), resembling those from the Limpopo River system whose drainage abuts on that of the Nata River. *A. wahlbergi* was not recorded from Lake Malawi itself by either Crowley *et al.* (1964) or Mandahl-Barth (1972) and its occurrence here is regarded as doubtful. Commenting on this, the latter author noted the species' presence in a roadside pool 5 km south of Monkey Bay. The shells (empty)

collected by Boswell (TM-11238) may have originated from a similar water body in the vicinity of Monkey Bay.

Braga (1952) illustrated a rather attenuated shell from Lagoa Bamba, Chibuto, Mozambique (L/H 2,36) which, although he gave no width measurement, appears otherwise comparable with the unusually obese specimens collected from Lagoa Pavi near Inhambane (MMK MOL-335) by H. A. Junod (L/H 2,13-2,21, mean 2,19) (not the same as those, also collected by Junod from Lagoa Pavi, recorded by Connolly 1925a). These shells may represent a lacustrine form occurring in the freshwater coastal lakes of the Mozambique peneplain.

The leech *Batrachobdella tricarinata* (Blanchard) (Branchiobdellidae) was found in the mantle cavities of two specimens from Ruacana in the Kunene River.

Aspatharia (Spathopsis) nyassaensis (Lea, 1864)

Fig. 2K

Material examined

'Lake Malawi', donor unknown, 1 specimen NM-A5367.

Mangoche (Fort Johnston) on Shire River between Lakes Malawi and Malombe, K. Fuller leg. 19 November 1971, 1 specimen.

Monkey Bay, Lake Malawi, M. N. Bruton leg. March 1973, 1 specimen; C. C. Appleton & D. H. Eccles leg. September 1976, live in sandy mud at about 3 m, 1 specimen.

An unmistakable large, thick-shelled species which is endemic to Lake Malawi and the Shire River (Mandahl-Barth 1972). It is much higher posteriorly than the other large *Aspatharia*, *A. wahlbergi*, and the specimens to hand have a lower L/H_{ad umbone} ratio of 1,70-1,96.

Aspatharia (Spathopsis) petersi (von Martens, 1859)

Although no specimens of this small, slender species are available from the area under discussion, Haas (1936) collected it from the Hunyani River 20 km south of Salisbury, Rhodesia. Connolly (1939) cites a record from Tete (the type locality) which lies on the lower Zambezi. *A. petersi* may be distinguished from *A. wahlbergi* by its much longer and narrower shell and hence its high L/H ratio of between 2,2 and 2,6 as opposed to 1,8 and 2,1 of the latter.

The distribution of this species is not well documented but it appears to be confined to the lower Zambezi as well as the eastwards flowing rivers of south-eastern Africa to about latitude 27°21'S. Specimens collected by B. Davies (Rhodes University) from Lake Tchal on the Incomati floodplain in Mozambique are, like *A. wahlbergi* from lakes in this region, longer in relation to height (L/H 2,30-2,57, mean 2,46) and more compressed than their counterparts from riverine environments. Data to hand suggest that the L/H ratios of shells from rivers range from 2,19 to 2,41 (mean 2,28).

Family Etheriidae

Etheria Lamarck, 1807*Etheria elliptica* Lamarck, 1807*Material examined*

Kunene River:

Kunene River at Otjinungua, Kaokoveld, W. D. Haacke leg. May 1966,
1 specimen + 2 valves, TM-93332.

Ontoruthu Falls (= Ondorusu Falls, 17°24'S 13°57'E), B. Kensley leg.
1973, 9 valves.

Yonge (1962) has discussed in detail the anatomy, evolution and life history of *Etheria elliptica* and concurs (Yonge 1962, 1978) with Haas (1969) and Thiele (1935) that *E. elliptica* is closely related to two other monotypic genera, the Colombian *Acostaea* and the Indian *Pseudomulleria*, and that these three comprise the family Etheriidae. The largest lower valve encountered measured $99,2 \times 49,0$ mm and the largest upper valve, $119,2 \times 82,4$ mm. One of the twelve upper valves available has the tube-like outgrowths (costae) typical of *E. elliptica* f. *tubifera* Sowerby. The only other record of *E. elliptica* from the Kunene River is by Germain in 1925 (cited by Haas 1936).

Only empty valves are available but M. J. Penrith (State Museum, Windhoek) has seen live specimens. He notes (*in litt.* 11 October 1976) that *E. elliptica* is very common in the Kunene from below the Ruacana Falls to the Foz du Cunene, where the last outcrops of rock occur (7 km from the mouth), and that it is usually found on the large boulders which in places form either banks or rapids in the river. However, it does not occur where flow is very fast, i.e. the shallower and narrower rapids. At the Ontorusu Falls the highest living animals were only a few centimetres below normal low water. He doubts whether the species occurs upstream of Ruacana and, if not, it would possess a distribution pattern which parallels that of some fish species. Dartevelle (1939) did not record *E. elliptica* from the upper Kunene.

Yonge (1962) noted that *E. elliptica* could be cemented to the substrate by either valve and that this occurred relatively late in its growth. The equivalve post-larva probably became attached (in the vertical position) initially by a byssus enabling it to withstand the high current velocities in which the adults are usually found. The later adoption of a horizontal posture was followed by cementation and growth as an inequivalve.

E. elliptica is widely distributed in tropical Africa and the Kunene shells represent its southernmost known locality.

DISCUSSION

Virtually nothing is known of the ecology of the freshwater bivalves of south-central Africa nor, indeed, of Africa generally. This is despite the fact that, although poor in numbers of species, the Unionacea of the river systems

under discussion are among the largest members of the benthos. Indeed, they may attain high population densities and may therefore constitute an important proportion of the benthic biomass. Relevant ecological studies include those of Pilsbry & Bequaert (1927) on the general malacology of the Congo River system, Fryer (1959, 1961) on the life-cycle of *Mutela bourguignati* (Ancey) in Lake Victoria, Marshall (1975) on the composition and distribution of the Unionacea of Lake MacIlwaine in Rhodesia, and Yonge (1962, 1978) on the settlement and cementation of *Etheria elliptica*. It is thus useful here to quote in full the locality notes accompanying specimens from the Kunene River and the Okavango delta (identifications inserted by the author).

M. J. Penrith (*in litt.* 11 May 1976) described the Kunene as a rather silt-laden river whos bed alternates between sand and rock. In sandy localities the channel is edged with *Phragmites*. Where rock is present it is either bare where the river is wide and slow-flowing (favourable *Etheria* habitats), or carpeted with *Hydrostachis* where it is fast flowing. There are fishes below the Ruacana Falls having affinities with rivers such as the Curoca and Quanza in Angola to the north.

At Ruacana B. F. Kensley collected four bivalve species from a single pool below the falls. His notes read: 'Hippo pool—small, muddy pool on Angolan side of river, bounded by sandy bar on the flowing river side and by reeds on the landward side. Maximum depth 0,9 m. Charophyte covering most of the bottom which consisted of a 2,5 cm layer of ooze, coarse sand below being black and anaerobic. *Caelatura kunenensis* most abundant, 6–10/m², in the ooze layer, *Mutela dubia* also lies (horizontally) in the first 2,5 cm of ooze. *Aspatharia pfeifferiana* and *A. wahlbergi* lay (vertically) about 7,6 cm below sand surface. *Mutela* and *Aspatharia* spp. were less common than *C. kunenensis*, seldom more than 1/m². Substrate surface scattered with dead shells, especially *C. kunenensis*. Openbill storks (*Anastomus lamelligerus* Temminck) observed feeding on bivalves. No water movement through pool and temperature higher than in flowing river.'

P. A. Reavell, who made a collection of bivalves near Maun in the Okavango delta, wrote: 'All specimens taken from the seasonally inundated area below perennial swamps. *Caelatura kunenensis* (typical form) prefers soft clay bottoms of streams in seasonally inundated area. Very common along Thamalakane River where in the dry season water may become stagnant with very low dissolved oxygen content. *Mutela dubia* usually together with *C. kunenensis* but more sporadic in distribution and of lower population density. *Aspatharia pfeifferiana* found only on clean, sandy bottoms where water was always flowing and dissolved oxygen content always high.' It is perhaps noteworthy that in many large *C. kunenensis* and *M. dubia* shells from the Thamalakane River erosion of the prismatic layer round the umbones and dorsal areas is unusually severe. This may be due to the action of aggressive carbon dioxide in the stagnant conditions which Reavell noted developed here.

These notes suggest that, while the bivalve species concerned are tolerant

of a wide range of dissolved oxygen concentration, *C. kunenensis* and *M. dubia* may prefer fine substrates such as clay and ooze whereas *Aspatharia* spp. may prefer coarser conditions.

Marshall (1975) found that in Lake MacIlwaine, a man-made impoundment on the Hunyani River in Rhodesia, *Mutela mabilli* (? = *M. dubia*) and *Caelatura mossambicensis* attained their greatest population densities (31/m² and 3/m² respectively) and largest sizes in the riverine part of the lake. This was tentatively taken as evidence that these bivalves remain essentially riverine animals after impoundment, an interpretation in agreement with Fryer (1961) who found that the fish *Barbus altianalis radcliffi* was more heavily parasitized by larval *Mutela bourguignati* in the Victoria Nile than in Lake Victoria itself. This may have been due to the fish being more abundant in the riverine environment and therefore easier for the larvae to locate. If so, it suggests an important role for host fish in determining the distribution and population density of at least some Unionacea in lacustrine environments. This aspect is also discussed by Jubb (1976) who adds that *U. caffer* glochidia probably parasitize both truly fresh-water fish species and those which are capable of moving from fresh to saline water. Thus *U. caffer* could, when parasitic on fish of the latter type, i.e. the widespread *Sarotherodon mossambicus* (Peters), be carried from one river system to another via the sea, suggesting that spread of species from one drainage to another might be effected by processes other than geomorphic ones (river capture). He notes, too, that adult *U. caffer* are tolerant of salinities up to 3°/oo but not 5°/oo.

The large perennial Kunene, Okavango and Zambezi rivers rise on the southerly part of the central Angolan highlands at about 1 700 m altitude; the smaller Cuvelai River, more seasonal in character, rises on the southernmost spur of this plateau, the Serra Encoco. Over much of the drainage of these rivers the topography is very flat, with gradients of 1:30 000 or less. While the Kunene flows westwards to the Atlantic Ocean and the Zambezi eastwards to the Indian Ocean, the intervening area includes three endoreic or inland drainage systems, the Cuvelai/Ekuma/Etosa, the Cubango/Okavango/Ngami/Makarikari and the Chobe/Liambezi/Linyanti. Where their beds are of sand or clay, these rivers broaden to create extensive floodplains where, in years of high rainfall, numerous low gradient valleys and channels (known in different areas as *oshanas*, *omurambas* or *mulapos*) become flooded and inundate vast areas of low-lying land. Water velocities in these seasonal watercourses seldom exceed 0,5 m/sec. (Stengel 1963: 375).

As far as a zoogeographical consideration of this malacofauna is possible, it is evident that the Kunene, Okavango and upper Zambezi River systems not only have several bivalve species in common but also constitute the southerly limits of the ranges of three west African Mutelidae, *Mutela dubia*, *Aspatharia pfeifferiana* and *Etheria elliptica*. Of the twelve unionacean species recorded from these systems the three Mutelidae listed above are predominantly west African species. Darteville (1939) attributed the similarity between the species

occurring in the upper Kunene and the Zambezi to capture of part of the drainage of the latter by the Kunene. *Caelatura kunenensis* is endemic to the western half of south-central Africa while *C. mossambicensis* and *Aspatharia petersi* are endemic to the eastern half. *Unio caffer* is a southern African endemic and *Aspatharia wahlbergi* enjoys a wide distribution in southern and east Africa. *Caelatura nyassaensis*, *C. hypsiprymna*, *Mutela alata* and *Aspatharia nyassaensis* are endemic to Lake Malawi.

Several examples exist of morphologically separable riverine and lacustrine forms of a species, e.g. *Caelatura kunenensis*, *Aspatharia wahlbergi* and *A. petersi*. Enough data are available to show (Fig. 3) that for *C. kunenensis* these differences are statistically significant ($p < 0.01$). This is probably a widespread phenomenon among freshwater Mollusca. Sutcliffe & Durrant (1977) have shown highly significant differences ($p < 0.001$) between the shell shapes of riverine and lacustrine populations of the limpet *Ancylus fluviatilis* (Muller) in England.

Similarities among the unionacean fauna of the river systems included in this study are probably due to connections between them during the Tertiary era (Gaigher & Mc. C. Pott 1973; Netterberg 1973) and to river capture. Connections still occur between the Okavango and upper Zambezi systems after exceptionally rainy seasons, when the waters of the Okavango flow via the Chobe/Linyanti rivers and the eastern Caprivi floodplain to the Zambezi at Kazungula, some 100 km upstream from the Victoria Falls. This floodplain is extremely flat, with a maximum height difference of only 20 m, so that in high flood the Zambezi may overflow in the reverse direction (Van der Waal 1974). Floods may occur more than once in each direction in a single rainy season.

Although the Kunene does not today overflow into Owambo even at high flood (Stengel 1963) there was before the breakthrough at the Ruacana Falls a previous connection with the Cuvelai/Etosha Pan system. Unfortunately, little bivalve material is available from this latter system. The upper tributaries to the Kunene, Okavango and Zambezi rivers not only lie close together, but their watersheds are ill-defined so that, in the dry seasons, it is difficult to tell in which direction they would flow (Wright 1963). Since these drainages were probably frequently connected during the pluvial periods of Pleistocene times, the spread of freshwater bivalves between them could readily occur. Fish might convey the parasitic stages of *C. kunenensis* and the Mutelidae from one drainage to another. Floods, too, can transport live bivalves. The author has found numerous large live *Unio caffer* scoured from the mud substratum of pools in a stream bed and carried by floods for considerable distances both downstream and away from its banks.

The apparent limits in the upstream distribution of *E. elliptica* in the Kunene River at the Ruacana Falls and of *C. mossambicensis* in the Zambezi at the Victoria Falls suggests that either large waterfalls or, since Ruacana is the most westerly of a series of falls, several smaller ones, may play important

roles in limiting bivalve distribution. This may be due to changes in substrate or to the barriers imposed by waterfalls on host fish distribution.

Except for *Caelatura mossambicensis*, and perhaps the little known *Aspatharia* (*A.*) *subreniformis* as well, the unionacean fauna of Lake Malawi consists of endemic forms with noticeably heavy shells (Mandahl-Barth 1972). This fauna seems to have affinities with the river systems to the west and south rather than with the other African Great Lakes to the north. Little is known of the Unionacea of the Shire River nor of how far south the Lake Malawi endemics are distributed within it. However, most occur in Lake Malombe as well and it is possible that the Murchison Falls (Shire River) act as a barrier here.

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6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierii Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

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Holotype

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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THE UNIONACEA
(MOLLUSCA, LAMELLIBRANCHIATA)
OF SOUTH-CENTRAL AFRICA

S-Hf-Capetown

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FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* 74: 627-634.

KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) 2: 309-320.

KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* 17 (4): 1-51.

THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Sud-Afrika* 4: 269-270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* 16: 269-270.

(continued inside back cover)

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UPPERMOST ALBIAN (*STOLICZKAIA DISPAR* ZONE)
AMMONITES FROM THE ANGOLAN LITTORAL

By

M. R. COOPER
&
W. J. KENNEDY

Cape Town Kaapstad

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By

M. R. COOPER

Queen Victoria Museum, Salisbury

&

W. J. KENNEDY

Geological Collections, University Museum, Oxford

(With 82 figures)

[MS. accepted 11 December 1978]

ABSTRACT

Rich, well-preserved collections of late Albian (*Stoliczkaia dispar* Zone) ammonites from the Angolan littoral provide the basis for discussion of the ontogenetic and intraspecific variation within *S.* (*Stoliczkaia*) *tenuis* Renz, *Tetragonites jurinianus* (Pictet), *Eogaudryceras italicum* Wiedmann & Dieni, *Desmoceras latidorsatum perinflatum* subsp. nov., *Phylloceras* (*Hypophylloceras*) *seresitense* Pervinquière, *Anisoceras haasi* sp. nov., and *Mortoniceras* (*Durnovarites*) *collignoni* sp. nov. Other important elements present include *Idiohamites dorsetensis* Spath, *I. pygmaeus* sp. nov., *I.* cf. *elegantulus* Spath, *Anisoceras armatum* (J. Sowerby), *A. perarmatum* Pictet & Campiche, *A. phillipsi* sp. nov., *Mortoniceras* (*Durnovarites*) *perinflatum* (Spath), *M.* (*D.*) *subquadratum* Spath, *M.* (*Angolaites*) *simplex* (Choffat), *M.* (*A.*) *gregoryi* (Spath), *Cantabrigites?* *curvatum* Renz, *Hysterocheras?* cf. *ootaturensis* (Stoliczka) and *Borissiakoceras* sp. nov. ? aff. *reymonti* (Brunnschweiler).

The faunas form the basis for discussion of the subdivisions of the *Stoliczkaia dispar* Zone, and a return to the simple division into subzones of *S.* (*Faraudiella*) *blancheti* below and *M.* (*Durnovarites*) *perinflatum* above is proposed.

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INTRODUCTION

Although Albian ammonites have long been known from Angola (Szajnocha 1884; Meunier 1887; Choffat *in* Choffat & De Loriol 1888), Paul Choffat was the first to record uppermost Albian ammonites when he described *Ammonites dispar* Choffat (*non d'Orbigny*) (= *Stoliczkaia tenuis* Renz) from the environs of Catumbela. Subsequently, many authors have reported on the presence of strata with *Ammonites dispar* (Mouta & Borges 1926, 1928; Mouta 1937, 1954, 1956; Mouta & O'Donnell 1933) and the presence of uppermost Albian strata in Angola is now well established. In contrast, the faunal constituents of these rocks are poorly known.

The collections which form the basis of this paper are from Porto Amboim, Cabo Ledo and Praia-Egito. The material from Porto Amboim comes from the lime kiln at the south side of the boat landing, and was collected mostly by C. W. Washburn on 22 July 1914, although some material from this locality, in the South African Museum, was described by Haughton (1924, 1925). Elements of this fauna were also described subsequently by Haas (1942), whose localities R28, R30 and 3041 have yielded an identical fauna in like preservation, with recrystallized test preserved. The fauna from Egito was collected by the senior author and comes from the coastal exposures at Praia-Egito where thinly-bedded limestone-shale alternations have yielded a rich fauna, mostly preserved as composite internal moulds. Faunas collected by the senior author from the Quissama Ridge, the promontory on which stands the Farol de Cabo Ledo, were obtained from road gravels and may represent more than one faunal horizon.

These faunas include a number of new species, and also populations, of *S.* (*Stoliczkaia*), *Mortoniceras* (*Durnovarites*), *E.* (*Eogaudryceras*), *Phylloceras* (*Hypophylloceras*), *D.* (*Desmoceras*), *Anisoceras* and *Tetragonites* which provide unique information on the intraspecific variation, development and morphology of these ammonites. Furthermore, the composition of the faunas provides an opportunity for discussion of the stratigraphic and geographic distribution of the late Albian *Stoliczkaia dispar* Zone fauna.

SYSTEMATIC PALAEOONTOLOGY

The following abbreviations are used to indicate the source of material:

BM British Museum (Natural History), London

SAM South African Museum, Cape Town

USNMNH U.S. National Museum of Natural History, Washington D.C.

Measurement abbreviations are as follows: D, diameter; H, whorl height; W, whorl width (intercostal unless otherwise specified); U, diameter of umbilicus between umbilical seams; W/H , whorl width/height ratio. All measurements are given in millimetres and dimensions, as a percentage of the diameter, follow in parentheses.

Class CEPHALOPODA Cuvier, 1797

Subclass AMMONOIDEA Zittel, 1884

Order PHYLLOCERATIDA Arkell, 1950

Superfamily PHYLLOCERATACEAE Zittel, 1884

Family *Phylloceratidae* Zittel, 1884

Subfamily *Phylloceratinae* Zittel, 1884

Genus *Phylloceras* Suess, 1865

Subgenus *Hypophylloceras* Salfeld, 1924

Type species *Phylloceras onoense* Stanton, 1895

Phylloceras (Hypophylloceras) seresitense Pervinqui re, 1907

Figs 1–2, 3I

Ammonites velledae Pictet & Campiche (*non* Michelin), 1860: 268, pl. 36 (fig. 8). Stoliczka, 1865: 116, pl. 59 (figs 1–3).

Phylloceras velledae (Michelin) Kossmat 1895: 12, pl. 1 (fig. 3). Boule, Lemoine & Th venin, 1906: 7, pl. 1 (figs 6, 11), fig. 2. Crick, 1907: 166, pl. 10 (figs 10–11). B se, 1923: 119, pl. 7 (figs 15–17). Spath, 1925b: 180. Besairie, 1936: 164, pl. 16 (fig. 1). Venzo, 1936: 66, pl. 5 (fig. 4). Haas, 1942: 146, pl. 27 (fig. 1), pl. 44 (fig. 1), fig. 19. Matsumoto, 1942: 676. Almela & Revilla, 1957: 17, pl. 3 (fig. 2). Anderson, 1958: 180, pl. 16 (fig. 4).

Phylloceras velledae var. *seresitense* Pervinqui re, 1907: 52; 1910: 9, pl. 1 (figs 1–3), fig. 2.

Phylloceras tanit Pervinqui re, 1907: 53, pl. 3 (figs 3–9), fig. 5.

Phylloceras angolaense Haughton, 1924: 85, pl. 1 (figs 1–2); 1925: 267, pl. 12 (figs 1–2).

Phylloceras seresitense Pervinqui re, Spath, 1923: 18, pl. 1 (fig. 2), pl. 2 (fig. 1). Collignon (*in* Besairie) 1936: 190, pl. 21 (figs 1–2). Fabre, 1940: 211, pl. 5 (fig. 1).

Phylloceras boulei Collignon, 1928: 144, pl. 15 (fig. 5), fig. 1.

Hyporbulites seresitensis (Pervinqui re) Breistroffer, 1947: 82.

Phylloceras (Hyporbulites) seresitense Pervinqui re, Collignon 1950: 66; 1963: 4, pl. 241 (fig. 1038), pl. 242 (fig. 1041).

- Hyporbulites seresitensis* var. *raynaudiensis* Collignon, 1956: 16, pl. 4 (fig. 1).
Neophylloceras seresitense (Pervinqui re) Matsumoto, 1959: 55, pl. 12 (figs 4–5), fig. 3.
 ? *Phylloceras* (*Euphylloceras*) *vohipalense* Collignon, 1962: 1, pl. 215 (fig. 940).
 ? *Phylloceras* sp. (*Ph. velledae*?) da Silva, 1962: 26, pl. 15 (figs 1–3).
Hypophylloceras seresitense seresitense (Pervinqui re) Wiedmann, 1962a: 142, pl. 8 (figs 1–2) fig. 8; 1962b: 249, pl. 16 (fig. 1).
Hypophylloceras seresitense tanit (Pervinqui re) Wiedmann, 1962a: 142; 1962b: 250, fig. 2.
Phylloceras (*Hypophylloceras*) *seresitense seresitense* Pervinqui re, Wiedmann, 1964: 221, pl. 15 (fig. 4), pl. 21 (fig. 1), fig. 52. Wiedmann & Dieni, 1968: 26. Kennedy & Klinger, 1977a: 364, pl. 4 (fig. 6), pl. 6 (fig. 4), pl. 7 (fig. 4), pl. 9. Renz, 1968: 17, pl. 1 (fig. 1).
Phylloceras (*Hypophylloceras*) *seresitense tanit* Pervinqui re, Wiedmann, 1964: 226, pl. 21 (figs 2–3), fig. 54. Wiedmann & Dieni, 1968: 26, pl. 1 (fig. 6), pl. 3 (figs 1–2).
Phylloceras (*Hypophylloceras*) *seresitense boulei* Collignon, Wiedmann, 1964: 224, pl. 20 (figs 2–3), fig. 53. Renz, 1968: 18, pl. 1 (fig. 2), figs 6a, 7c. F rster, 1975: 140, pl. 1 (fig. 1), fig. 27.
 ? *Phylloceras* (*Hypophylloceras*) *seresitense vohipalense* Collignon, F rster, 1975: 139, fig. 26.
 ? *Phylloceras serum* var. *perlobata* Zwierzycki (*non* Sayn), 1913: 323, figs a–c.
 ? *Phylloceras* ex aff. *ramosi* Meek, Collignon, 1928: 1, pl. 1 (figs 2–4).
 ? *Phylloceras* aff. *tanit* Pervinqui re, Matsumoto, 1942: 674, fig. 2.
Phylloceras cf. *seresitense* Pervinqui re, Wright & Wright, 1951: 12.
 ? *Phylloceras* cfr. *semistriatum* Choffat (*non* d'Orbigny), 1903: 17, pl. 1 (fig. 10).

Material

Ten specimens, SAM–6527, USNMNH 236897–236904, 237013, all with recrystallized shell preserved, and all from Porto Amboim.

Description

The coiling is very involute, with a narrow, crater-like umbilicus (6–7% of the diameter). The whorl section is strongly compressed, elliptical ($w/H = 0,55–0,67$). The flanks are slightly convex, with maximum width just below midflank, converging to a narrow, evenly rounded venter. Ornament comprises fine, flexuous lirae, very faint or completely effaced on the inner half of the flanks (faint growth striae suggest they were prorsiradiate there), recurving at about midflank so as to pass straight or slightly backwards across the venter. On USNMNH 236897 there are about 128 lirae per half-whorl. None of the present specimens shows the sutures.

Measurements

No.	D	H	W	w/H	U
USNMNH 236897	37	21(57)	13(35)	0,62	2,6(7)
„	26,5	15,5(58)	±8,5(32)	0,55	
USNMNH 236898	52	30,5(59)	17,5(34)	0,57	3(6)
„	35	19(54)	11(31)	0,58	?
USNMNH 236900	15	8(53)	5(33)	0,63	1,1(7)
„	11	5,5(50)	3,7(34)	0,67	?
USNMNH 236901	17	10(59)	6,5(38)	0,65	1,0(6)
USNMNH 236902	21	12(57)	7,7(37)	0,64	?

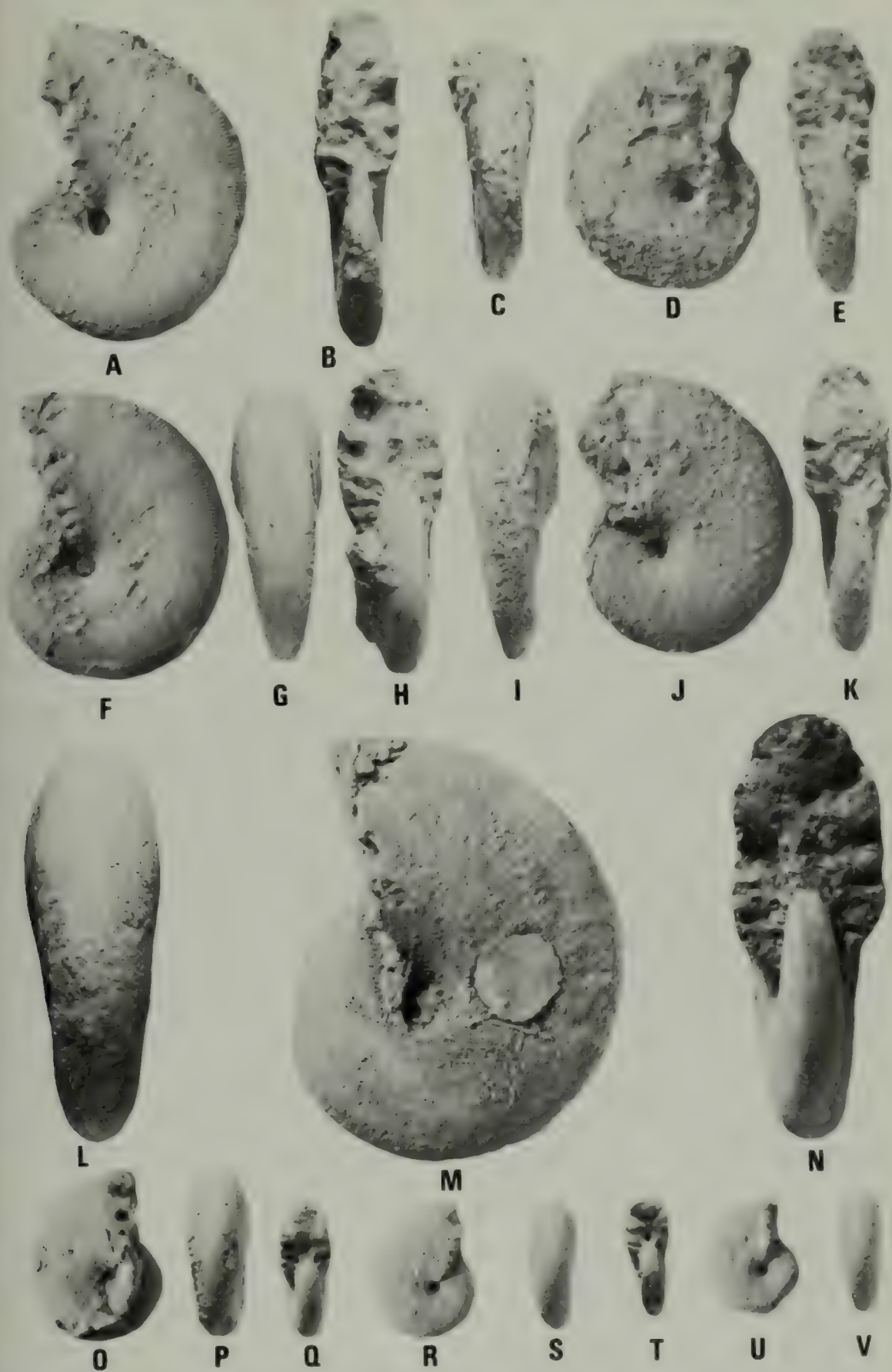


Fig. 1. *Phylloceras* (*Hypophylloceras*) *seresitense* Pervinqui re. A-B. USNMNH 236899. C-E. USNMNH 236904. F-H. USNMNH 236897. I-K. USNMNH 236903. L-N. USNMNH 236898. O-P. USNMNH 236902. Q-S. USNMNH 236901. T-V. USNMNH 236900. $\times 1$.

Intraspecific variation

Wiedmann (1964: 221) recognized three subspecies within *P. (H.) seresitense*:
P. (H.) seresitense seresitense—whorl section moderately compressed, whorl width to height ratio up to 0,65. Umbilicus very narrow.

P. (H.) seresitense boulei Collignon—whorl section very compressed ($W/H = 0,50-0,57$), with very narrow umbilicus.

P. (H.) seresitense tanit—whorl section compressed, but with moderately open umbilicus.

The most noteworthy variation in the population before the writers is in the degree of inflation of the whorls. As can be seen from Figure 2 the variation in this respect ($W/H = 0,55-0,67$) includes individuals of all of Wiedmann's (1964) subspecies and, since they are all broadly contemporaneous (ranging from Aptian to Cenomanian), appear to have little biological significance. The authors find, therefore, the application of the subspecies *boulei* and *tanit* inappropriate to the present collection.

Discussion

The holotype of *Phylloceras angolaense* Haughton is in the South African Museum, SAM-6527. The specimen is entirely septate and is replaced by crystalline calcite.

The shell is strongly compressed and very involute, with a very narrow, deep umbilicus. The flanks are slightly convex, almost flat, and converge towards the narrow, evenly rounded venter (Fig. 3I). Maximum width is about one-quarter of the way up the flanks. Ribbing is very faint on the inner half of the flanks, although growth striae suggest it was prorsiradiate here. On the outer half of the flanks, the ribs recurve so as to become almost radial. The ribbing is very fine, with fourteen ribs in a distance of 10 mm along the venter on the adoral quarter of the outer whorl.

There are no features by which *P. angolaense* may be satisfactorily distinguished from *P. seresitense* and consequently the authors follow Wiedmann (1962a, 1962b) in regarding it as a junior subjective synonym of Pervinquière's species.

Phylloceras velledae (Michelin) (Wiedmann 1964: 209, pl. 11 (fig. 1), pl. 13 (fig. 4), pl. 21 (fig. 4), fig. 49) typically differs from the present species in having more convex flanks, with much coarser, more flexuous lirae, and a suture which shows diphyllic saddles in immaturity rather than tetraphyllic saddles as in *P. (H.) seresitense*.

Hypophylloceras yeharai Nakai & Matsumoto (1968: 4, pl. 1 (figs 1-3), pl. 3 (fig. 1)) is based upon crushed material said to differ from *P. (H.) velledae* in its more compressed whorls (? enhanced by crushing) and less numerous and broader lirae. Kennedy & Klinger (1977a) have recently demonstrated the wide range of variation within contemporaneous populations of *P. (H.) velledae* and

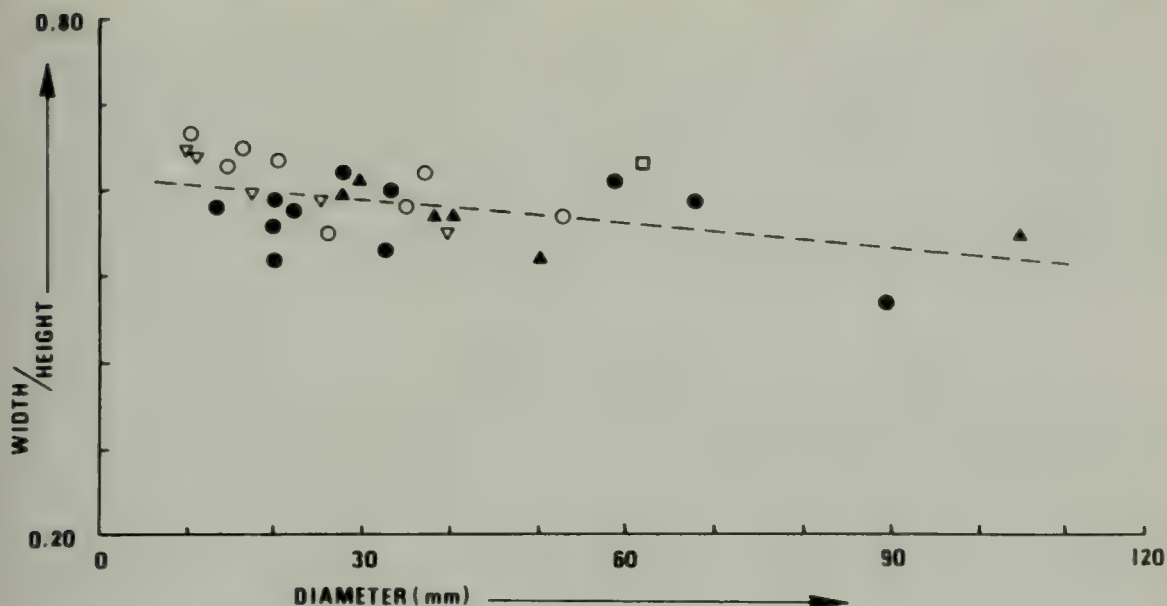


Fig. 2. Plot of inflation (whorl width/height ratio) versus diameter for *Phylloceras seresitense* Pervinqui re, showing the unsatisfactory separation of subspecies. Circles = present Angolan material; dots = *P. seresitense tanit* Pervinqui re; square = holotype of *P. angolaense* Haughton; open triangles = *P. seresitense seresitense* Pervinqui re; black triangles = *P. seresitense boulei* Collignon. (Data after Stoliczka 1865, Spath 1923, Wiedmann 1962, Collignon 1963, Wiedmann & Dieni 1968, Renz 1968, F rster 1975, and Kennedy & Klinger 1977.)

figured examples (1977a: pls 10–11) as coarsely ribbed as the Japanese material, suggesting that *P. (H.) yeharai* may be within the limits of variation of *P. (H.) velledae*.

Occurrence

Phylloceras (Hypophylloceras) seresitense ranges from Upper Aptian to Middle Cenomanian, and is known from southern France, Switzerland, southern England, Spain, Tunisia, Algeria, Sardinia, the Balearics, southern India, Japan, Alaska, California, Mexico, Angola, Zululand, possibly Tanzania, and Madagascar.

Order LYTOCERATIDA Hyatt, 1889

Superfamily LYTOCERATACEAE Neumayr, 1875

Family Tetragonitidae Hyatt, 1900

Genus Tetragonites Kossmat, 1895

Types species *Ammonites timotheanus* Pictet, 1848

Discussion

Wiedmann (1973) has provided the most recent discussion of the Albian to Cenomanian members of this genus, recognizing three species groups. The group of *T. rectangularis* possesses persistent constrictions and a straight umbilical suture, and includes *T. rectangularis* Wiedmann, *T. subtimotheanus*

Wiedmann, *T. kitchini* (Krenkel), *T. subbeticus* Wiedmann, *T. marrei* Thomel and *T. blaisoni* Collignon. In the group of *T. timotheanus* (Pictet), constrictions are present only at an early growth stage, whilst the umbilical suture is retracted. To this group Wiedmann (1973) assigned *T. timotheanus* (Pictet), *T. balmensis* Breistroffer, and *T. nautiloides* (Pictet). Forms lacking constrictions at all growth stages are referred to the group of *T. jurinianus* (Pictet).

Tetragonites (Tetragonites) collignoni Breistroffer, 1940

Ammonites timotheanus Stoliczka (*non* Mayor), 1865: 146, pl. 73 (figs 3–4, 6).

Tetragonites collignoni Breistroffer, 1940: 110. Murphy, 1967a: 66, pl. 5 (figs 2–5), fig. 36. Förster, 1975: 147, pl. 1 (fig. 5) (with synonymy).

Tetragonites subtimotheanus Wiedmann, 1962a: 131; 1973: 592, pl. 1 (fig. 5), pl. 2 (fig. 2), pl. 3 (figs 1–5), pl. 7 (fig. 8), fig. 2 (with synonymy).

Tetragonites blaisoni Collignon, 1964: 31, pl. 324 (fig. 1448). Wiedmann, 1973: 601, pl. 1 (fig. 4), pl. 6 (figs 5–7), fig. 7 (with synonymy).

Material

One specimen, USNMNH 236916, preserved as an internal mould, from Porto Amboim.

Description

Shell involute, somewhat inflated, with a depressed, trapezoidal whorl section ($w/h = 1.21$). Umbilicus narrow (22% of the diameter), deep, with steep, almost vertical umbilical walls. Umbilical shoulder evenly rounded, with flattish flanks converging towards a broad, slightly convex venter which rounds somewhat in maturity. There are two distinct constrictions in a distance equal to the whorl height on the last portion of the outer whorl (representing part of the body chamber), although the number of constrictions per whorl is unknown. The constrictions are markedly prorsiradiate across the inner flanks, recurving strongly in the region of the ventrolateral angulations to cross the venter with a prominent concave sinus.

Measurements

No.	D	H	W	w/h	U
USNMNH 236916	44	21.5(49)	$\pm 26(59)$	1.21	$\pm 9.5(22)$

Discussion

Problems concerning the specific identification of constricted tetragonitids become very clear from the recent literature concerning this group (Wiedmann 1962a, 1962b, 1973; Collignon 1963, 1964; Murphy 1967a, 1967b; Wiedmann & Dieni 1968; McLearn 1972; Förster 1975; Kennedy & Klinger 1977b). Förster (1975) has suggested that *T. subtimotheanus* and *T. blaisoni* are junior subjective synonyms of *T. collignoni*. Wiedmann (1973) rejected the latter name because it

was based upon a pyritic nucleus only 14 mm in diameter (although he retains *T. kitchini* and *T. subbeticus* as valid species even though the types are only 18 and 16 mm in diameter respectively), considering it a *nomen dubium*. Because the authors are at present unhappy with Wiedmann's (1973) fine delimitation of *T. subtimotheanus* Wiedmann, *T. rectangularis* Wiedmann, *T. blaisoni* Collignon, and *T. kitchini* (Krenkel), all of which are broadly contemporaneous, they have some sympathy with Förster's (1975) view in assigning the present material to *T. collignoni*.

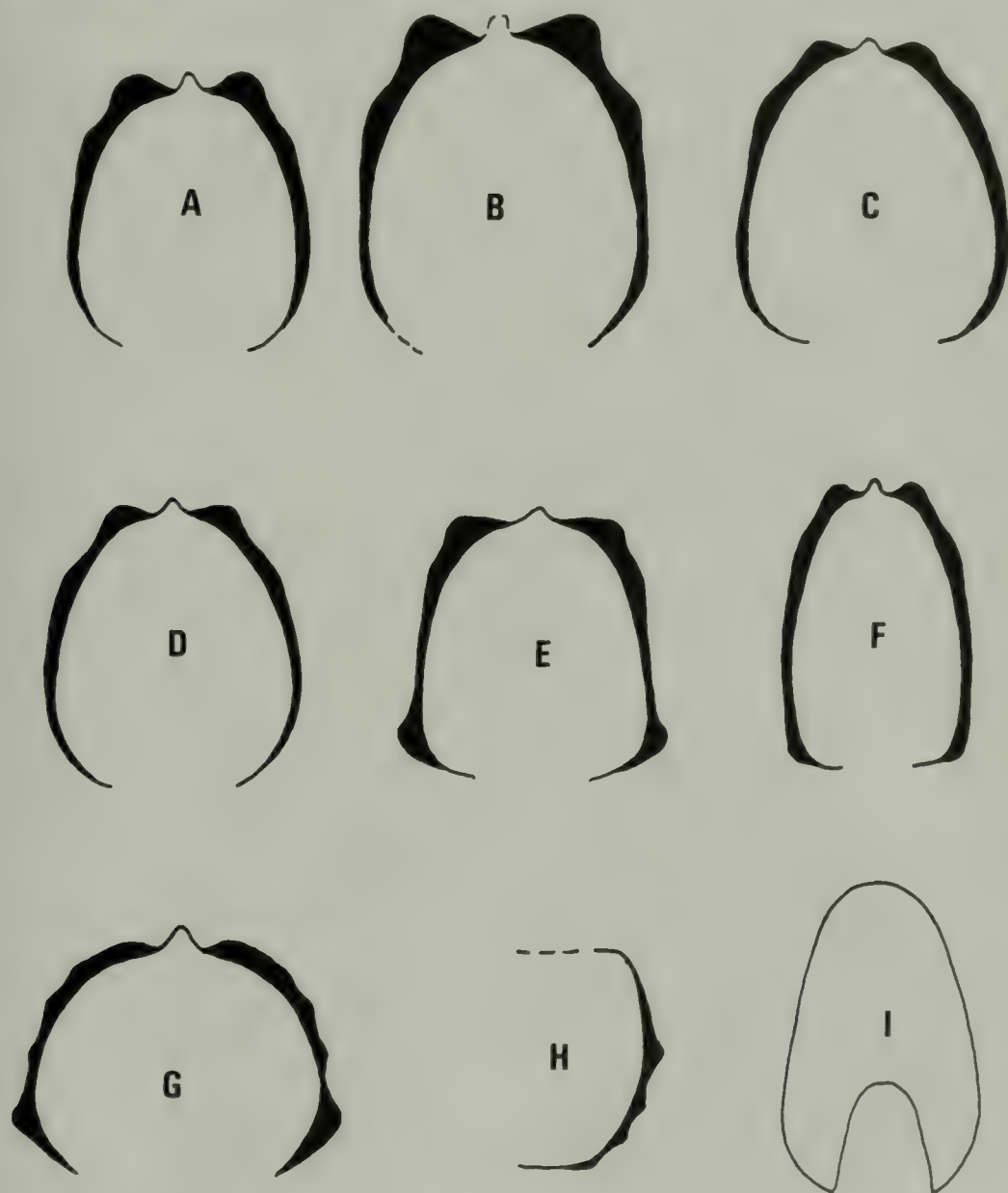


Fig. 3. A-D. *Mortoniceras* (*Angolaites*) *simplex* (Choffat). A. SAM-PCA4613. B. SAM-PCA4774. C. SAM-PCA4590. D. SAM-PCA4609. E-F. *Drakeoceras* cf. *dellense* Young. E. SAM-PCA4662. F. SAM-PCA4800. G. *Mortoniceras* (*Durnovarites*) *perinflatum* (Spath), SAM-PCA4587. H. *Mariella* (*Mariella*) cf. *oehlerti* (Pervinqui re), SAM-PCA4798. I. *Phylloceras* (*Hypophylloceras*) *seresitense* (Pervinqui re), the holotype of *P. angolaense* Haughton, SAM-6527. $\times 1$.

Occurrence

Tetragonites collignoni ranges from the Lower Albian to the Middle Cenomanian, and is known from Madagascar, southern India, Zululand, Alaska, British Columbia, and Oregon.

Tetragonites (Tetragonites) kitchini (Krenkel, 1910)

Fig. 4

? *Ammonites timotheanus* Whiteaves (*non* Mayor), 1876: 41, pl. 3 (fig. 2).

Desmoceras (Puzosia; Latidorsella?) kitchini Krenkel, 1910: 226, pl. 22 (fig. 8).

Tetragonites kitchini (Krenkel), Wiedmann 1962a: 171. Murphy, 1967a: 33, pl. 2 (figs 11–14), figs 15–16. Wiedmann, 1973: 599, pl. 1 (fig. 7), pl. 6 (figs 1, ?2–4), figs 5, ?6.

Tetragonites hulenensis Murphy, 1967a: 54, pl. 6 (figs 16–19), pl. 7 (figs 3, 6–8, 10), figs 28–30. Murphy, 1967b: pl. 4 (figs 8–9).

? *Tetragonites* aff. *kitchini* (Krenkel), McLearn 1972: 26, pl. 4 (figs 4–5).

Material

A single specimen, SAM-PCA3125, from low in the coastal cliffs immediately north of the estuary at Praia-Egito (low *dispar* Zone).

Description

The shell is moderately involute (umbilicus 31,5% of the diameter) and partially retains recrystallized shell. The whorl section is subtrapezoidal, almost subquadrate, as wide as high ($w/h = 1,00$), with slightly converging flanks and a flattish, slightly convex venter. The umbilicus is rather narrow and deep, with steep umbilical walls and subrounded umbilical shoulders. The ventrolateral shoulders are evenly rounded. Maximum width is at the umbilical shoulder.

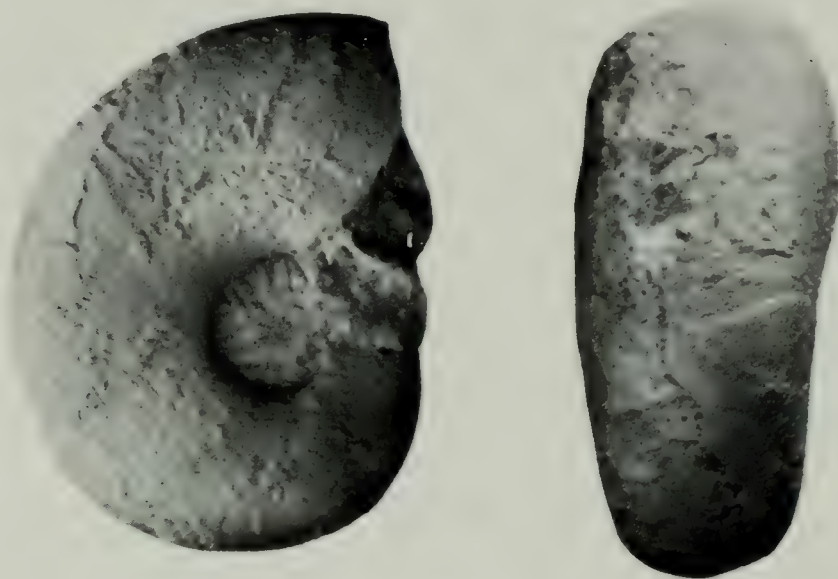


Fig. 4. *Tetragonites kitchini* (Krenkel). Lateral and ventral views of SAM-PCA3125, partially retaining recrystallized test. $\times 1$.

There would appear to have been about seven slightly flexuous (prorsiradiate concave in the terminology of Murphy (1967a)), strongly prorsiradiate constrictions on the outer whorl, which cross the venter with a concave-adoral sinus. The suture line was not observed.

Measurements

No.	D	H	W	W/H	U
SAM-PCA3125	54	25(46)	25(46)	1,00	17(31,5%)

Discussion

Tetragonites kitchini differs from all other contemporaneous species of constricted *Tetragonites* in having less strongly inflated whorls with an almost quadrate whorl section. However, there appear to be intermediate forms to *T. subtimotheanus* Wiedmann and *T. rectangularis* Wiedmann, and the population structures of these species require investigation to fully validate their specific separation.

Occurrence

Tetragonites kitchini is known from the upper Lower Albian of Tanzania, California, Alaska, and perhaps British Columbia, and from the Middle or Upper Albian of Madagascar, and the uppermost Albian of Angola.

Tetragonites (Tetragonites) jurinianus (Pictet, 1847)

Figs 5–6

Ammonites jurinianus Pictet (in Pictet & Roux), 1847: 297, pl. 3 (fig. 3). D'Orbigny, 1850: 124.

Ammonites timotheanus Pictet & Campiche (non Mayor), 1860: 289 (pars).

Lytoceras (Tetragonites) epigonum Boule, Lemoine & Thévenin (non Kossmat), 1906: 186, pl. 3 (fig. 1).

? *Lytoceras (Tetragonites) timotheanum* Pervinquière (non Mayor), 1907: 74 (pars.), pl. 3 (fig. 24 only).

Lytoceras (Tetragonites) jurinianum (Pictet) Jacob, 1908: 19, pl. 1 (fig. 12).

Latidorsella latidorsata Jacob (non Michelin), 1908: 35, pl. 5 (fig. 1 only).

Lytoceras (Tetragonites) zacatecanus Böse, 1923: 127, pl. 9 (figs 11–17).

Tetragonites jurinianus (Pictet) Spath, 1923: 26. Roman, 1938: 43. Breistroffer, 1940: 112.

Wiedmann, 1962a: 176, pl. 14 (fig. 2), figs 37–38. Almela & Revilla, 1957: 20, pl. 4 (fig. 3).

Murphy, 1967a: 23, pl. 2 (figs 1–4); figs 10–11. Renz, 1968: 19, pl. 1 (figs 6–7), figs 6d,

7a–b. Wiedmann & Dieni, 1968: 48, pl. 4 (fig. 4), pl. 5 (fig. 4). Wiedmann, 1973: 608,

pl. 8 (figs 3–4).

? *Tetragonites brazoensis* Böse, 1927: 203, pl. 1 (figs 2–7).

Tetragonites jurinianus var. *angolana* Haas, 1942: 170, pl. 44 (fig. 3), pl. 45 (fig. 1).

Tetragonites timotheanus Matsumoto (non Mayor), 1959: 78, fig. 16.

Tetragonites jurinianus angolanus Haas, Wiedmann, 1973: 609.

Material

Ten specimens, USNMNH 236915, 236917–21, 236977–79, all with recrystallized shell preserved, and all from Porto Amboim.

Description

Shell inflated, involute, with a slightly depressed, trapezoidal whorl section in juveniles ($W/H = 1,00-1,29$), the venter becoming rounded in maturity. Umbilicus narrow (16–30% of the diameter), deep, with almost vertical walls and evenly rounded umbilical shoulders. The flanks are flattened, with maximum width close to the umbilical shoulder, and converge towards the venter. Up to 25 mm diameter, the venter is flattened, very slightly convex, whereafter it becomes rounded and the ventrolateral angulations disappear. At this stage the whorl section is broadly ovate. Constrictions are lacking at all observed growth stages.

Measurements

No.	D	H	W	W/H	U
USNMNH 236915	52,5	25,5(49)	$\pm 28(53)$	1,10	10(19)
USNMNH 236917	38,5	20(52)	$\pm 22(57)$	1,10	$\pm 9(23)$
„	30	14,5(48)	16(53)	1,10	9(30)
USNMNH 236918	43	19(44)	22,3(52)	1,17	9,8(23)
USNMNH 236919	16	7,5(47)	8,5(53)	1,13	4(25)
USNMNH 236920	18	8(44)	10(55)	1,25	$\pm 4(22)$
USNMNH 236921	21	10(48)	$\pm 10(48)$	1,00	5(24)
USNMNH 236977	17,5	6,8(39)	8,5(49)	1,25	4,5(26)
USNMNH 236978	17	7(41)	9(53)	1,29	4,7(28)

*T. jurinianus**angolanus*

(holotype)	105	56(53)	51(48)	0,91	17(16)
„	63	32(51)	34(54)	1,06	?

Intraspecific variation

The intraspecific variation seen in *Tetragonites jurinianus* shows features which have an important bearing on the classification of tetragonitids in general. The wide range of inflation within juveniles far exceeds the range of variation admitted by Wiedmann (1973) within the constricted tetragonitids as a whole, and population studies may show his subdivisions of the group to be utilitarian rather than biologically significant.

As can be seen from Figure 6, there is not only a distinct decrease in the umbilical ratio with growth, but there is also an ontogenetic increase in the height of the whorls, which become progressively less inflated.

Wiedmann (1973) maintained *T. jurinianus angolanus* as a separate subspecies by virtue of its narrower umbilicus (16% versus 23% of the diameter in *T. jurinianus jurinianus*), high-oval whorl section and large size. It appears, however, that these differences result from a comparison of different ontogenetic stages, and the authors include *T. jurinianus angolanus* in the synonymy of *T. jurinianus sensu stricto*.



Fig. 5. *Tetragonites (Tetragonites) jurinianus* (Pictet). A-B. USNMNH 236918. C-D, G. USNMNH 236921. E-F. USNMNH 236978. H-J. USNMNH 236977. K-M. USNMNH 236917. N-P. USNMNH 236919. Q-S. USNMNH 236920. $\times 1$.

Discussion

As diagnosed by Wiedmann (1973: 606), *Tetragonites nautiloides* (Pictet) does not have constrictions beyond 10 mm diameter and thus closely approaches *T. jurinianus*. Indeed, the present material all exceeds this diameter and could, therefore, equally well be assigned to *T. nautiloides*. However, Murphy (1967a) has noted that constrictions are present to 27 mm diameter in topotype material of *T. nautiloides* when there is considerable difficulty in distinguishing this

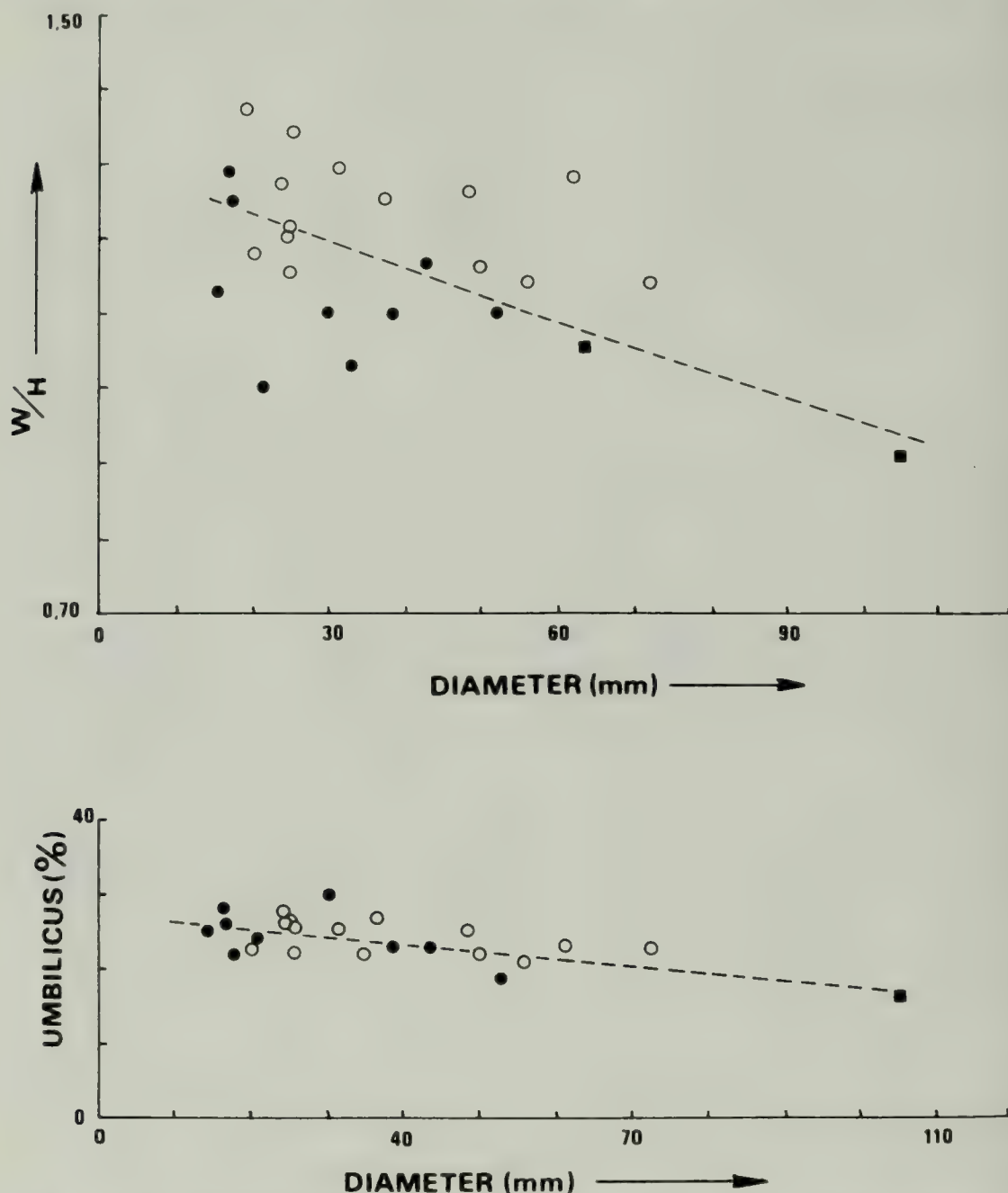


Fig. 6. Plot of inflation (whorl width/height ratio) and umbilical ratio against diameter for examples of *Tetragonites jurinianus* (Pictet). Dots = present Angolan material; squares = the holotype of *T. jurinianus angolanus* Haas; circles = material described by Wiedmann (1962, 1973), Murphy (1967a), Wiedmann & Dieni (1968).

species from some constricted tetragonitids, e.g. *T. rectangularis* Wiedmann. Wiedmann's (1973) diagnosis of *T. nautiloides* is difficult to support, since some of his figured specimens (pl. 8 (figs 2, 5)) clearly show weak constrictions at 22 and 27 mm diameter respectively, suggesting that this species may better be included in the *T. rectangularis* group.

Occurrence

Tetragonites jurinianus ranges from Middle Albian to Lower Cenomanian, and is recorded from Switzerland, France, Sardinia, Mallorca, Madagascar, Angola, Mexico, and California.

Family Gaudryceratidae Spath, 1927

Subfamily Gaudryceratinae Spath, 1927

Genus *Eogaudryceras* Spath, 1927

Type species *Ammonites numidus* Coquand, 1880

Discussion

Eotetragonites was originally separated (Breistroffer 1947) from *Eogaudryceras* by the possession of strong constrictions throughout ontogeny, and a suture with irregularly bifid saddles. However, Wiedmann (1962b: 35) has noted the occurrence of species which show combinations of these characters, consequently treating *Eotetragonites* as a subgenus of *Eogaudryceras*. As defined by him (1962b), *E.* (*Eogaudryceras*) has initially trapezoidal whorls which become rounded in maturity and are ornamented by fine, flexuous lirae, whereas *E.* (*Eotetragonites*) has quadrate juvenile whorls and lacks liration.

Eogaudryceras (*Eogaudryceras*) *italicum* Wiedmann & Dieni, 1968

Figs 7–11

Eogaudryceras (*Eogaudryceras*) *italicum* Wiedmann & Dieni, 1968: 34, pl. 1 (fig. 8), fig. 6.

Material

Ten specimens, USNMNH 236905–236914, all with recrystallized shell preserved, and all from Porto Amboim.

Description

Up to 23 mm diameter: shell evolute, compressed, with a wide, shallow umbilicus (30–41 % of the diameter) and steep umbilical walls which merge imperceptibly with the strongly convex flanks. The whorl section is oval, depressed ($W/H = 1.00–1.36$), with a broadly rounded venter. The outer whorl conceals about 55 per cent of the preceding whorl. The earliest whorls are very finely lirate, almost smooth to the naked eye, with sporadic, rather distinct, prorsiradiate collars.

24–45 mm diameter: the shell form is much as at the earlier growth stages, except that the flanks flatten slightly and the whorl section changes from slightly depressed to almost quadrate. At this stage the lirae are visible to the naked eye; they arise at the umbilical seam and pass forwards (prorsiradiate) on the lower third of the flanks. Thereafter they recurve slightly, only to flex forwards again before crossing the venter. At intervals one or two adjacent lirae are strengthened, presumably corresponding to the collars of the earliest whorls. The lirae become flat-topped, band-like, much broader than the interspaces, and of variable thickness at this stage.

Greater than 46 mm diameter: in maturity the whorls become flat-sided and compressed ($W/H = 0,66-0,80$), with an elliptical whorl section and narrowly rounded venter. The umbilicus is moderately wide (26–33 % of the diameter), shallow, with steep umbilical walls and evenly rounded umbilical shoulders. Maximum width is at about mid-flank. At this growth stage the irregular band-like ribs are split by fine, threadlike grooves. In the largest specimen (still septate at 82 mm diameter) there are still occasional strengthened ribs, followed by a slightly deeper intercostal groove. These may correspond to the collars of the earliest whorls.



Fig. 7. *Eogaudryceras* (*Eogaudryceras*) *italicum* Wiedmann & Dieni. Reconstruction of juvenile and adult shells. $\times 1$.



Fig. 8. *Eogaudryceras* (*Eogaudryceras*) *italicum* Wiedmann & Dieni. A-B. USNMNH 236905.
C-E. USNM 236908. $\times 1$.

Measurements

No.	D	H	W	w/H	U
USNMNH 236905	81	37,5(46)	25(31)	0,66	21(26)
„	56	25(45)	19,5(35)	0,78	17,5(31)
USNMNH 236906	34	13(38)	15,5(45)	1,19	±10(29)
USNMNH 236907	±47	±21(45)	±18(38)	0,86	15,5(33)
USNMNH 236908	71	33,5(47)	±27(38)	0,80	19(27)
USNMNH 236909	26	11(42)	11(42)	1,00	8(31)
„	19,5	8(41)	8(41)	1,00	±5,5(28)
USNMNH 236910	24	9(38)	8(38)	1,00	8,5(35)
„	18	6,5(36)	7(39)	1,08	7(39)
USNMNH 236911	15	5,5(37)	6(40)	1,09	5(30)
USNMNH 236912	22	8(36)	9(41)	1,13	8(36)
USNMNH 236913	17	5,5(32)	±7,5(44)	1,36	7(41)
USNMNH 236914	25	9(36)	±11(44)	1,22	±8,5(34)
<i>E. (E.)italicum*</i>	±50	25(50)	19(38)	0,76	±14(28)
<i>E. (E.)aenigmum*</i>	58,3	28,3(48,5)	24(41,5)	0,86	14(24)
<i>E. (E.)b. bourritianum*</i>	33	14(42)	20(60)	1,43	10(30)
<i>E. (E.)b. hispanicum*</i>	47	20(42)	22(47)	1,10	13(28)
<i>Gaudryceras</i> aff.					
<i>madraspatanum</i>					
Spath (<i>non</i> Stoliczka)	28	11,8(42)	11,8(42)	1,00	10(36)

* Asterisks mark holotypes or neotypes.

Intraspecific variation

The most noteworthy feature of the present material is the great change in whorl section with growth. The earliest whorls show a wide range in inflation ($w/H = 1,00-1,36$) but, with continued growth, the shell becomes increasingly high-whorled and the whorl section becomes strongly compressed (Fig. 11). At the same time there is a slight, but distinct, tendency for the umbilical ratio to decrease (Fig. 11).

Discussion

E. (Eogaudryceras) italicum Wiedmann & Dieni is based upon a smooth, fragmentary internal mould from the Upper Albian of Sardinia. It agrees precisely with the present material in whorl section and relative proportions; lack of liration may simply be a reflection of different preservation.

Gaudryceras aff. *madraspatanum* (Stoliczka) (Spath 1923: 22, pl. 1 (fig. 4)) is based upon a smooth phosphatic internal mould from the Cambridge Greensand of southern England. In relative proportions it falls well within the range of variation of the present Angolan material, and the writers would tentatively refer it, therefore, to *E. italicum*.



Fig. 9. *Eogaudryceras* (*Eogaudryceras*) *italicum* Wiedmann & Dieni. A-C. USNMNH 236905. D-F. USNMNH 236906. G, K-L. USNMNH 236910. H-J. USNMNH 236909. M-O. USNMNH 236912. $\times 1$.

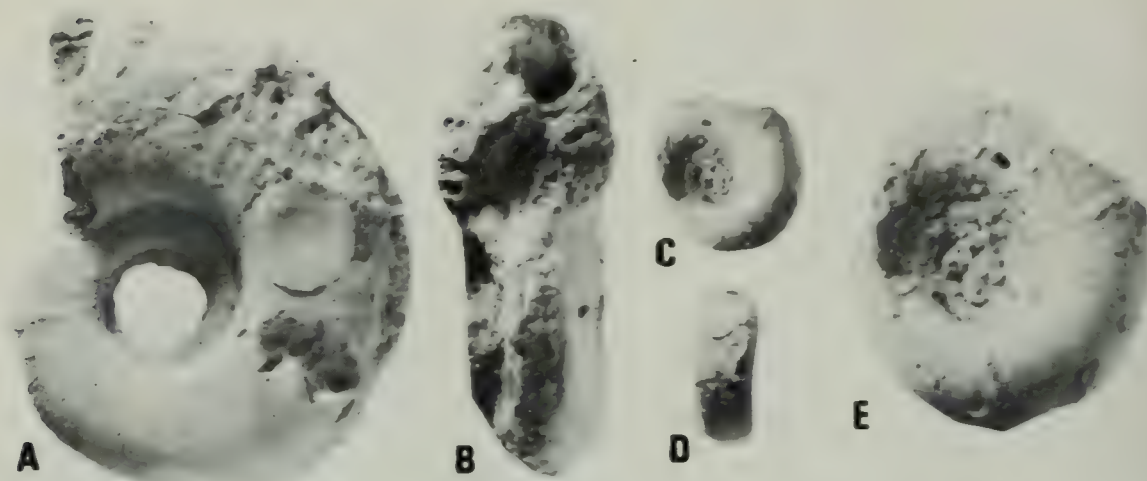


Fig. 10. *Eogaudryceras* (*Eogaudryceras*) *italicum* Wiedmann & Dieni.
A-B. USNMNH 236907. C-E. 236911. A-D $\times 1$, E $\times 2$.

The present sample is the largest single population of an *E.* (*Eogaudryceras*) species yet described, and shows a wide range of ontogenetic and intraspecific variation. In view of this wide range of variation, it seems probable that population studies will reduce in number the twelve species currently assigned to this subgenus, viz. *E.* (*E.*) *numidum* (Coquand), *E.* (*E.*) *intermedium* (Fallot), *E.* (*E.*) *vocontianum* (Fallot), *E.* (*E.*) *elegans* Basse, *E.* (*E.*) *shimizui* Breistroffer, *E.* (*E.*) *llosetae* Breistroffer, *E.* (*E.*) *turgidum* Breistroffer, *E.* (*E.*) *schoenbergense* Collignon, *E.* (*E.*) *bourritianum* (Pictet), *E.* (*E.*) *aenigmum* (Haas) and *E.* (*E.*) *muntaneri* Wiedmann.

Of other Upper Albian species of *Eogaudryceras* (*Eogaudryceras*), Wiedmann (1962a: 154) selected a neotype for *E.* (*E.*) *bourritianum* (Pictet) (*in* Pictet & Roux 1848: 298, pl. 4 (fig. 1)) and divided it into two chronological subspecies: *E.* (*Eogaudryceras*) *bourritianum bourritianum*, from the uppermost Albian (*dispar* zone) of south-west France is characterized by its strongly depressed whorl section ($W_H = 1.43$), involute form ($U = 30\%$ of the diameter) and smooth whorls (the neotype is preserved as an internal mould and hence the lack of ornament may not be a diagnostic character). It differs from the Angolan material in its much more depressed whorl section and narrower umbilicus; *E.* (*Eogaudryceras*) *bourritianum hispanicum* Wiedmann (1962a: 155, pl. 12 (fig. 6), fig. 15) is a low Upper Albian form (associated with *Hysterocheras* and *Mortonicer*) which was said to differ from the typical form in its less depressed, trapezoidal whorl section ($W_H = 1.10$), flattened venter, and greater involution ($U = 28\%$ of the diameter). It differs from *E.* (*E.*) *italicum* in being more involute, having a slightly more depressed whorl section and a flattened venter.

E. (*Eogaudryceras*) *aenigmum* (Haas) (1942: 167, pl. 42 (fig. 3), pl. 44 (fig. 2), fig. 24) is from the Upper Albian of Angola. Crushed material assigned to this species, in the British Museum (Natural History), comes from Praia do Jombe

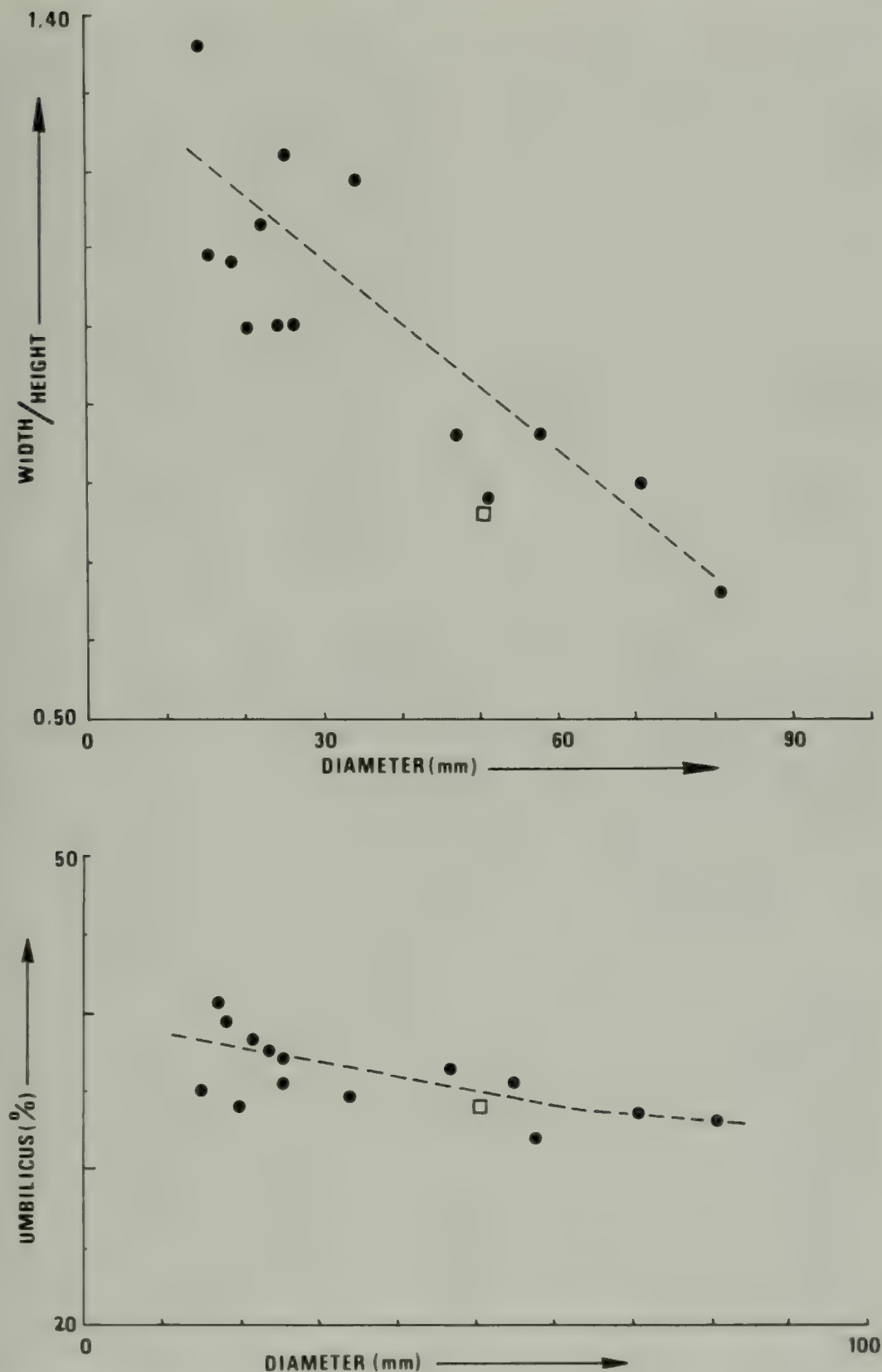


Fig. 11. Plot of inflation and umbilical ratio against diameter for *Eogaudryceras italicum* Wiedmann & Dieni. Dots = present Angolan material; square = holotype (after Wiedmann & Dieni 1968).

where it is associated with a low Upper Albian fauna which includes *Prohystero-ceras wordiei* Spath, *Beudanticeras beudanti* (Brongniart) and *Mortoniceras* cf. *inflatum* (J. Sowerby). It is thus a contemporary of *E. (E.) bourritianum hispanicum*. The style of ornament is difficult to judge from Haas's (1942) illustration, although the specimen is clearly lirate (it has shell preserved). Although its whorl width/height ratio is closely comparable to *E. italicum* (? due to crushing), it is much more involute ($U = 24\%$ of the diameter). Haas's (1942) whorl section of the species shows inner whorls with a strongly fastigate to keeled venter which suggest his material to be crushed. If true, this species may prove to have priority over *E. (E.) bourritianum hispanicum*.

Occurrence

E. (Eogaudryceras) italicum is currently known from the uppermost Albian of Sardinia, Angola, and possibly southern England.

Suborder ANCYLOCERATINA Wiedmann, 1966

Superfamily ANCYLOCERATAEAE Meek, 1896

Family Ancyloceratidae Meek, 1876

Subfamily Anisoceratinae Hyatt, 1900

Genus *Anisoceras* Pictet, 1854

Type species *Hamites saussureanus* Pictet, 1847

Anisoceras (Anisoceras) perarmatum Pictet & Campiche, 1861

Figs 12A–H, 13C–D, 14A–C, 15C–F, 16B

Hamites armatus J. de C. Sowerby (*non* J. Sowerby), 1850: pl. 29 (fig. 13).

Anisoceras perarmatum Pictet & Campiche, 1861: 65, pl. 48 (figs 7–8), pl. 49 (figs 1–3, 5–7). Pictet, 1861: 21. Ooster, 1863: 19. Pictet & Renevier, 1866: 103. Jukes-Browne, 1875: 288. Barrois, 1878: 271. Renevier, 1890: 340. Boule, Lemoine & Thévenin, 1907: 35. Ganz, 1912: 121. Spath, 1921: 289. Böse, 1923: 144. Diener, 1925: 73. Spath, 1925*b*: 191. Barbu, 1932: 16. Roman, 1938: 52. Spath, 1939: 548, pl. 59 (figs 1–3), pl. 61 (figs 3–7), fig. 192. Breistroffer, 1947: 62. Reymont, 1955: 12, pl. 1 (fig. 1). Collignon, 1963: 50, pl. 259 (figs 1126–1127). Swensen, 1963: 67, pl. 4 (figs 1, 3, 7). Dieni & Massari, 1963: 798. Clark, 1965: 25, pl. 6 (figs 1, 3, 7). Wiedmann & Dieni, 1968: 65, pl. 6 (fig. 4), pl. 7 (fig. 9), figs 38–39. Renz, 1968: 74, pl. 13 (fig. 5a–c), pl. 14 (figs 1, 3, 5), figs 27a, 28g.

Hamites (Anisoceras) perarmatus (Pictet & Campiche) von Hauer, 1861: 644, pl. 2 (figs 2–4). Pervinquière, 1907: 85.

Hamites (Anisoceras) saussureanus von Hauer (*non* Pictet), 1861: 644, pl. 2 (fig. 1).

Anisoceras armatus Stoliczka (*non* J. Sowerby), 1866: 174, pl. 81 (figs 8–10), pl. 82 (fig. 1).

Hamites perarmatus (Pictet & Campiche) Neumayr, 1875*a*: 30; 1875*b*: 898.

? *Anisoceras vracense* Renz, 1968: 75, pl. 16 (fig. 2), fig. 27b.

Anisoceras perarmatum simplex Renz, 1968: 75, pl. 13 (fig. 7), pl. 14 (fig. 4), fig. 27k.

? *Anisoceras pseudopunctatum* Pictet & Campiche, 1861: 74, pl. 52 (figs 1–3). Breistroffer, 1947: 62. Renz, 1968: 79, pl. 16 (figs 1, 3, 5). Wiedmann & Dieni, 1968: 72.

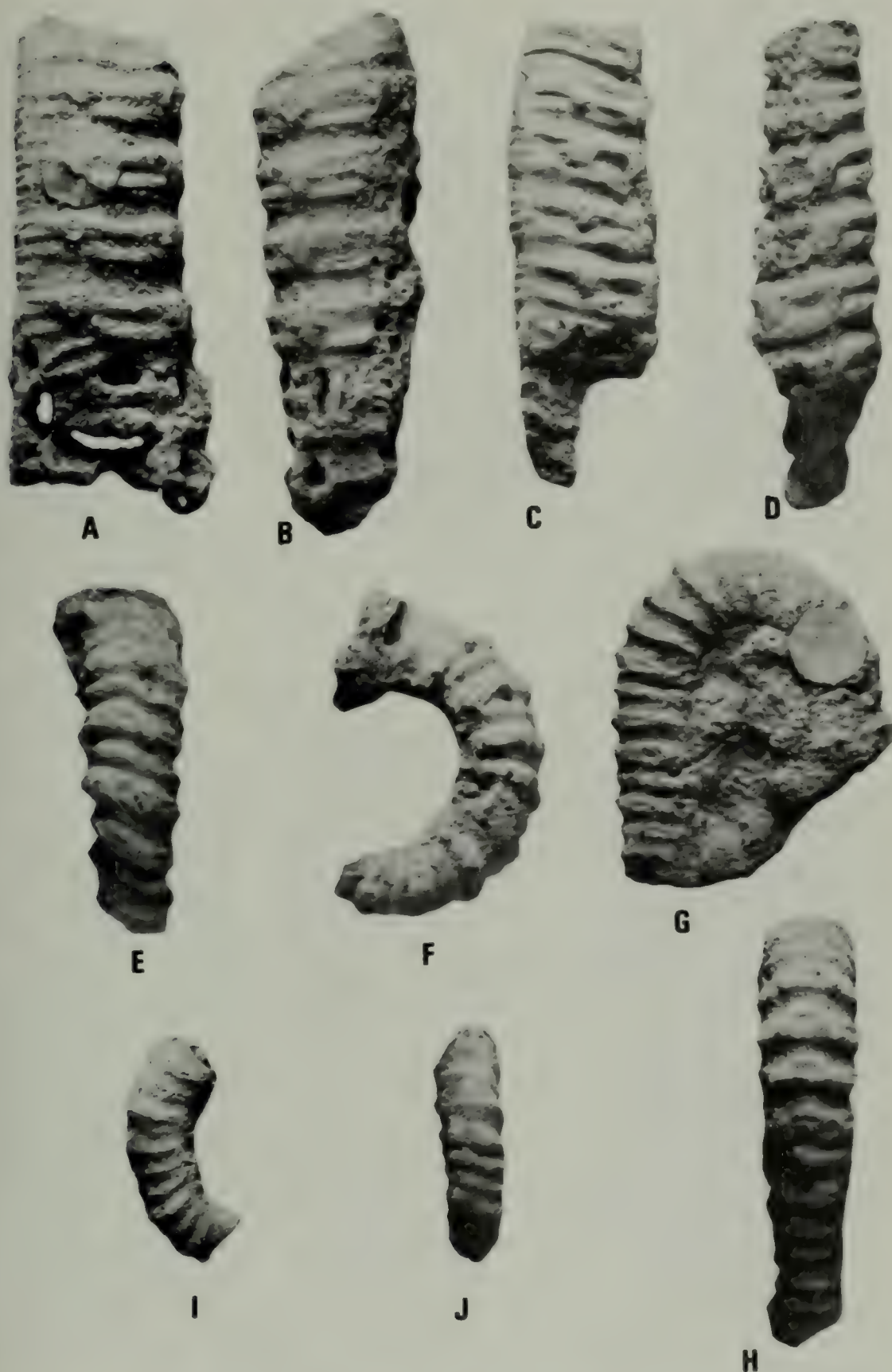


Fig. 12. A-H. *Anisoceras perarmatum* Pictet & Campiche. A-B. USNMNH 236928. C-D. USNMNH 236929. E-F. USNMNH 236944. G-H. USNMNH 236940. I-J. *Anisoceras* sp. juv., USNM 236745. $\times 1$.



Fig. 13. A-B. *Anisoceras armatum* (J. Sowerby), USNMNH 236934. C-D. *Anisoceras perarmatum* Pictet & Campiche, USNMNH 236931. $\times 1$.

Material

Twenty-seven specimens, SAM-PCA2940, 2950, 2956, 3115, 3122, 3143, 3148, 3152, 3193, 3214, 3243, 3283, 3285, 3299, 3339, 3352, 3355, 3358, 3361 and 3391, all from Egito, SAM-PCA4801, 4804 from Cabo Ledo and USNMNH 236928-29, 236931, 236933, 236940, and 236944 from Porto Amboim, either retaining recrystallized shell or preserved as composite internal moulds.

Description

Whorl section varies from almost circular in specimens replaced by calcite to slightly elliptical in those crushed individuals preserved as composite internal moulds.

Ornament comprises small dorsolateral to lateral tubercles and the septate bases of prominent ventrolateral spines, between which strong ribs are looped in pairs. There are sporadic non-tuberculate intercalatories between looped ribs. The main ribs are also looped across the venter, and split into fine riblets, thirteen per three dorsolateral tubercles, on the dorsum. On the body chamber there may be one to two simple ribs (SAM-PCA3143, 3148) between looped ribs, whilst on the final shaft of USNMNH 236940, the button-and-loop ribbing is lost, and all ribs become single.

Discussion

Amongst contemporaneous species of *Anisoceras*, only *A. saussureanum* and *A. armatum* closely approach this species. Differences are noted under the discussion of *A. armatum*.

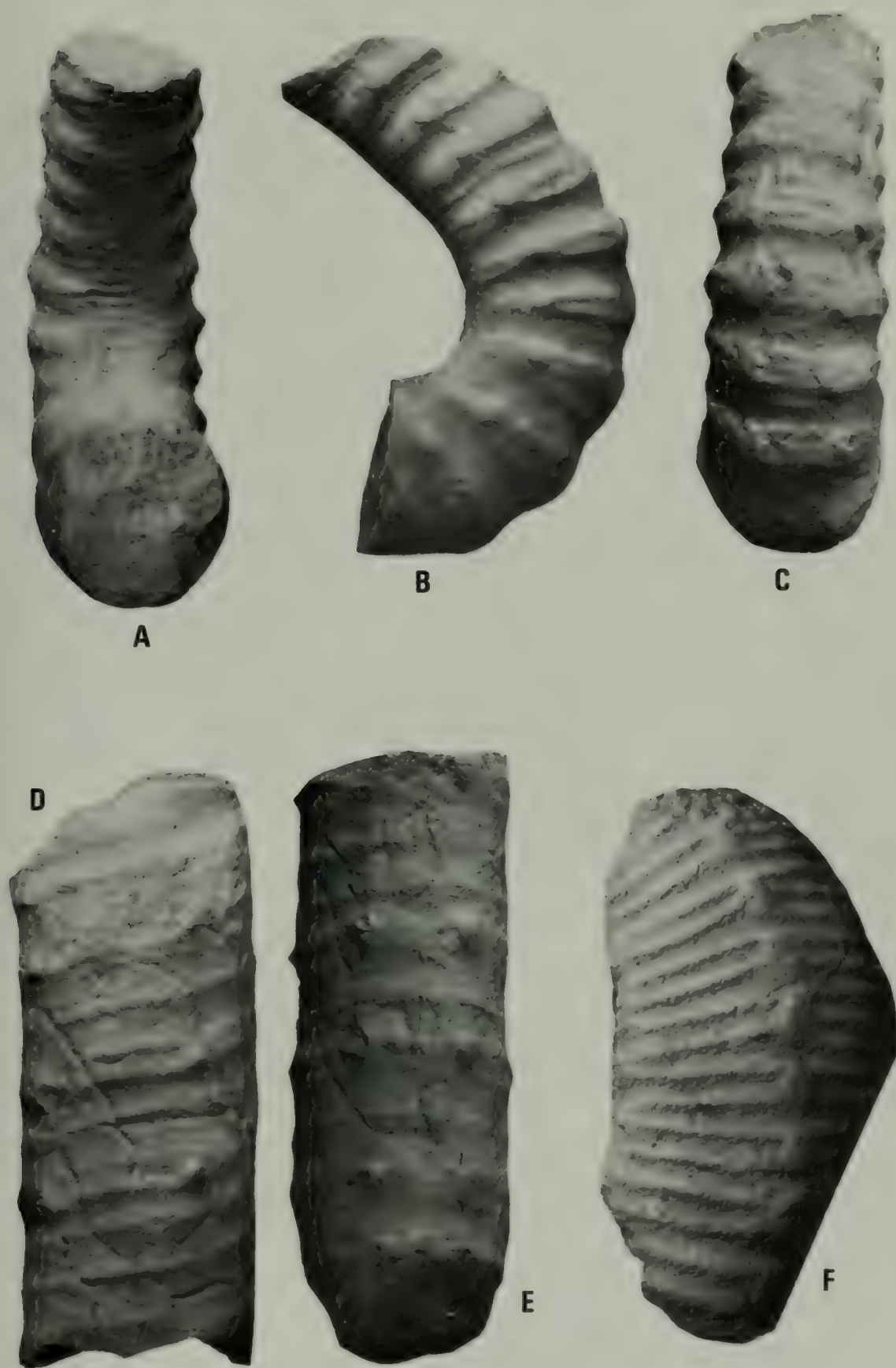


Fig. 14. A-C. *Anisoceras perarmatum* Pictet & Campiche. Dorsal, lateral and ventral views of SAM-PCA3115. D-E. *Anisoceras* cf. *armatum* (J. Sowerby). A fragment of a body chamber, SAM-PCA3287, which may belong here. F. *Anisoceras* sp. Oblique lateral view of SAM-PCA3220. $\times 0,75$.

Anisoceras vraconense Renz (1968: 75, pl. 16 (fig. 2), fig. 27b) differs from *A. perarmatum* in having most ribs simple and much weaker dorsolateral tubercles. This species may be based upon a fragment of the final shaft of *A. perarmatum*, since the ribbing simplifies on the body chamber.

Anisoceras charlottense Anderson (1958: 209, pl. 11 (fig. 3)) has a circular whorl section and very prominent looped ribs separated by three to four simple, finer intercalatories. It may be conspecific with the low Upper Albian *A. salei* Clark (1958: 1079, pl. 140 (fig. 3)).

Anisoceras perarmatum simplex Renz (1968: 75, pl. 13 (fig. 7), pl. 14 (fig. 4), fig. 27k) is simply a variant based on a small body chamber fragment.

Anisoceras pseudopunctatum Pictet & Campiche (1861: 74, pl. 52 (figs 1–3)) is based on material which, like *A. perarmatum simplex*, has also lost button-and-loop ribbing, and may equally be an intraspecific variant.

Occurrence

Anisoceras perarmatum is a typical *dispar* Zone species known from England, France, Switzerland, Sardinia, Tunisia, Nigeria, Madagascar, southern India, Texas, and Angola.

Anisoceras (Anisoceras) armatum (J. Sowerby, 1817)

Figs 13A–B, 14D–E, 16A, C, E, I, 17–19

Hamites armatus J. Sowerby, 1817: 153, pl. 168. De Haan, 1825: 152, no. 2. Buckland, 1837: 65, pl. 44 (figs 9–10). Brown, 1837: 2, pl. 2 (fig. 6). Romer, 1840: 94, pl. 15 (fig. 2). D'Orbigny, 1842: 547, pl. 135.

Non Hamites armatus Mantell (*non* J. Sowerby), 1822: 121, pl. 23 (figs 3–4) (= *A. plicatile*).

Baculina armata (J. Sowerby) Fleming, 1828: 250.

? *Hamites undulatus* Brown (*non* Forbes), 1837: pl. 2 (fig. 11).

Non Hamites armatus J. de C. Sowerby (*non* J. Sowerby), 1850: pl. 29 (fig. 13) (= *A. perarmatum*).

? *Hamites armatus* J. Sowerby, Dixon, 1851: pl. 29 (fig. 13).

Anisoceras armatum (J. Sowerby) Pictet & Campiche, 1861: 62, pl. 48 (figs 1–2, 4, 6). Spath, 1939: 543, pl. 59 (fig. 6), pl. 60 (fig. 1), pl. 61 (?figs 9–11), pl. 62 (?fig. 5), fig. 191. Swensen, 1963: 66, pl. 3 (fig. 4), pl. 4 (?fig. 6). Clark, 1965: 25, pl. 5 (fig. 4), pl. 6 (?fig. 6), fig. 7a. Renz, 1968: 75, pl. 15 (figs 1, 3), figs 27d, 28a.

? *Hamites (Anisoceras) armatus* J. Sowerby, von Hauer, 1861: 644, pl. 1 (figs 9–10).

Non Anisoceras armatum Stoliczka (*non* J. Sowerby), 1866: 174, pl. 81 (figs 8–10), pl. 82 (fig. 1) (= *A. perarmatum*).

Hamites (Anisoceras) armatus J. Sowerby, Kossmat, 1895: 149.

? *Anisoceras armatum* (J. Sowerby) Choffat, 1905: 41, pl. 1 (fig. 6).

Non Hamites (Anisoceras?) armatus Pervinquière (*non* J. Sowerby), 1907: 84, pl. 4 (figs 2–3) (= ? *A. exoticum*).

Anisoceras aff. *armatum* (J. Sowerby) Adkins, 1920: 69.

? *Hamites* cf. *armatus* J. Sowerby, Passendorfer, 1921: 237.

Anisoceras cf. *armatum* (J. Sowerby) Böse, 1923: 143, pl. 10 (figs 22–24). Haughton, 1924: 94. Clark, 1958: 1080, pl. 139 (fig. 2).

Non Anisoceras aff. *armatum* (J. Sowerby) Spath, 1925b: 190 (= *A. raynaudi*).

Anisoceras picteti Spath (*non* Matheron), 1926a: 432. Spath, 1939: 554, pl. 59 (fig. 4), pl. 61 (fig. 8), pl. 63 (figs 3, 8), fig. 194. Renz, 1968: 76, pl. 13 (figs 8–9), pl. 14 (figs 6–9), pl. 15 (fig. 4), figs 27c, 28f.

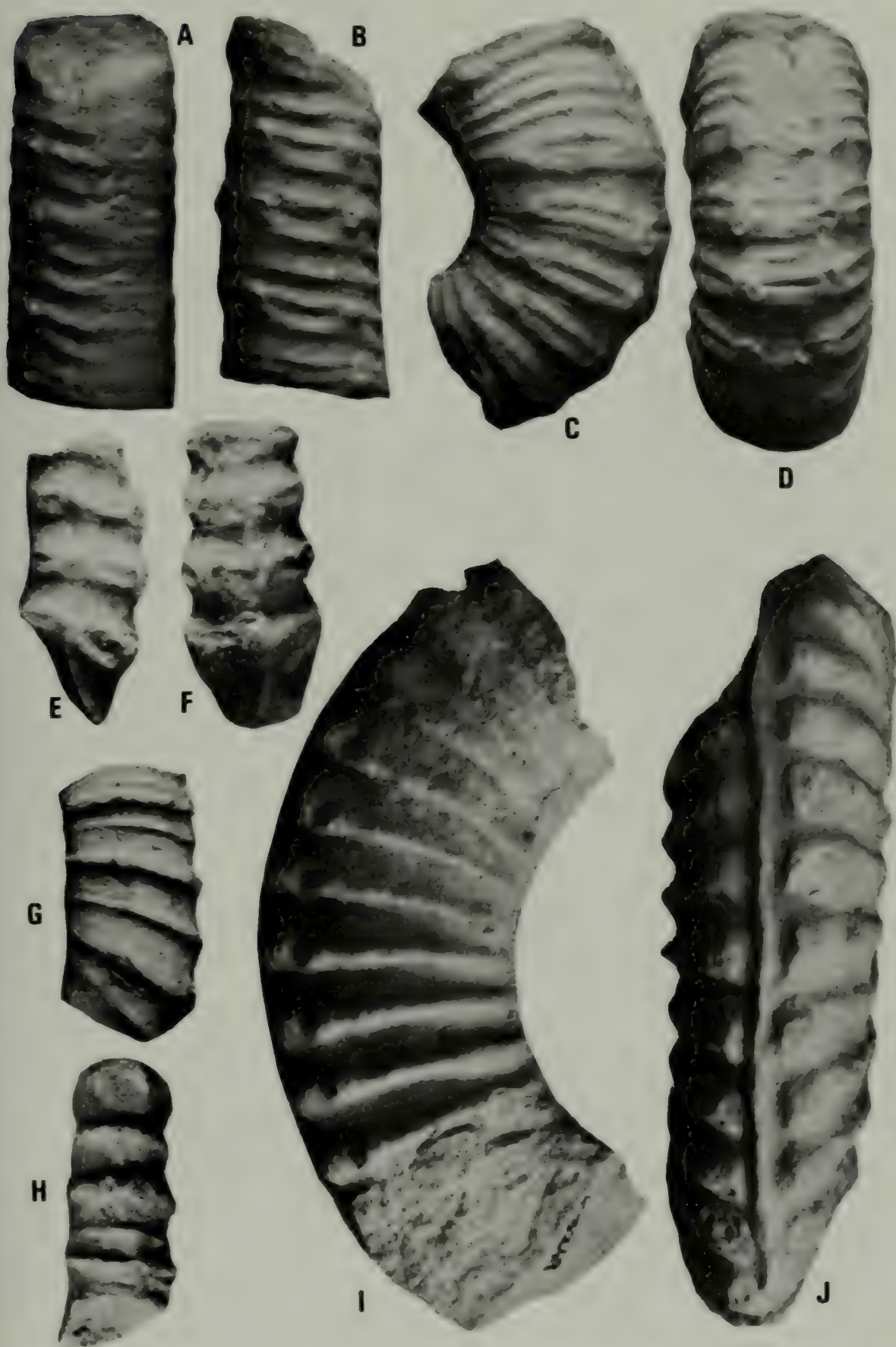


Fig. 15. A-B. *Anisoceras* sp. Oblique dorsolateral and lateral views of SAM-PCA3301 from Egito. C-F. *Anisoceras perarmatum* Pictet & Campiche. C-D. Ventral and lateral views of SAM-PCA3154. E-F. Lateral and ventral views of SAM-PCA4801. G-H. *Anisoceras* sp. An indeterminate body chamber fragment from Egito, SAM-PCA2942. I-J. *Mortonicer* (*Angolaites*) *simplex* (Choffat). Lateral and ventral views of SAM-PCA3249. A-D, G-H $\times 0.75$, E-F, I-J $\times 1$.

- ? *Hamites* aff. *armatus* J. Sowerby, Scott, 1926: 80. Böse, 1928: 146. Adkins, 1928: 24.
 ? *Anisoceras* cf. *armatum* (J. Sowerby) Passendorfer, 1930: 667.
 ? *Non Hamites* (*Anisoceras*) *armatus* Collignon (*non* J. Sowerby), 1932: 20, pl. 4 (fig. 1).
Anisoceras saussureanum var. *spinosa* Haas, 1942: 192, pl. 46 (figs 1–3), fig. 30.
Non Anisoceras armatum Haas (*non* J. Sowerby), 1942: 189, fig. 29 (= *A. tropicale*).
Anisoceras jacobi Breistroffer, 1946: 310; 1947: 62. Wiedmann & Dieni, 1968: 67, pl. 6 (fig. 13), fig. 41.
 ? *Anisoceras* aff. *picteti* Spath, Kennedy, 1971: 13, pl. 3 (fig. 6), pl. 7 (fig. 10).
 ? *Non Anisoceras armatum* (J. Sowerby) Kennedy, 1971: 14, pl. 5 (fig. 11).

Material

Fourteen specimens, SAM-PCA2932, 2947, 2953, 3174, 3364, and 3398 from Egito, USNMNH 236930, 236934, 236936–37, 236939, and ?236952 from Porto Amboim, and SAM-PCA4606 and 4610 from Cabo Ledo.

Description

Shell form suggests initial coiling in an open planispiral, straightening in maturity. The whorl section is approximately circular.

The ornament is rather variable, comprising slightly rursiradiate to slightly prorsiradiate looped ribs, between which are generally one, sometimes two, simple intercalatories. Looped ribs are ornamented with small pointed dorso-lateral tubercles and the septate bases of prominent ventrolateral spines. All ribs are of more or less equal strength. Across the dorsum the ribs divide into fine riblets and are accompanied by intercalatories.

In USNMNH 236939, which is taken to represent an early portion of the spire of the species, main ribs are weakly looped and are separated by two to three intercalatories. In USNMNH 236952, the largest specimen (which is, however, still septate), the whorl section is slightly compressed, oval, and there is generally only one intercalatory between looped ribs, although even these are sometimes absent.

Discussion

Anisoceras armatum is a widely-cited but poorly understood species, and in consequence the holotype is refigured here (Fig. 17). As noted by Spath (1939: 546), this is a crushed, composite internal mould which shows the following features: the penultimate shaft has distinct looped ribs separated by only one non-tuberculate intercalatory which is of approximately the same strength as the looped ribs. At this stage there are about five ribs in a distance equal to the whorl height (allowing for post mortem crushing). On the hook, the preservation is poor, but the looped ribs clearly break up so as all to become single on the final non-septate shaft. At this stage there are still only about five ribs in a distance equal to the whorl height, and most of the ribs are of approximately the same strength. The dorsolateral tubercles are still present in maturity, although weak and irregularly developed.

It is clear from the above description, and comparison with Sowerby's original illustration (cf. Spath 1939, fig. 191), that this species has been mis-

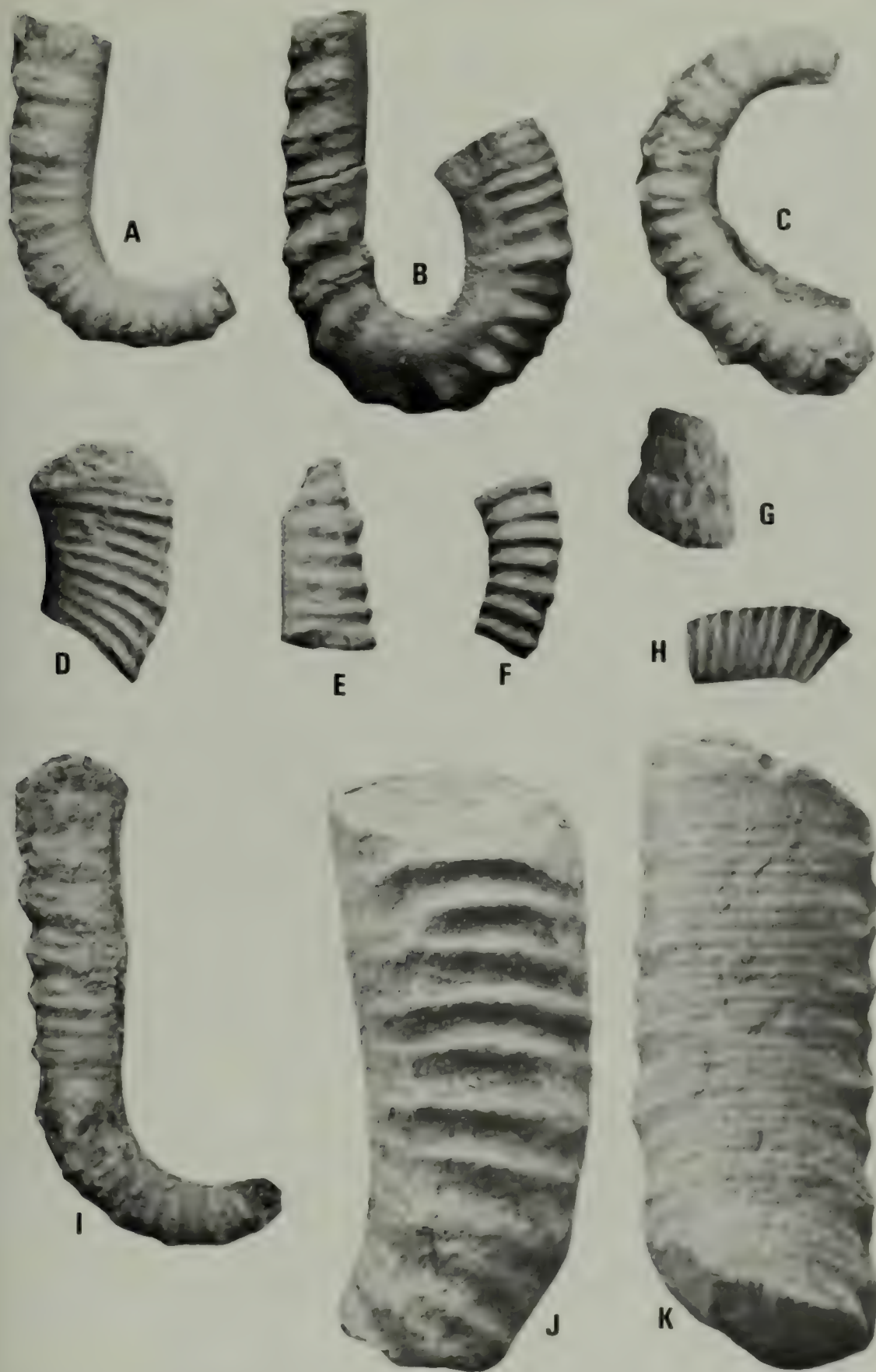


Fig. 16. A, C, E, I. *Anisoceras armatum* (J. Sowerby). A. SAM-PCA5470. C. SAM-PCA5471. E. SAM-PCA5473. I. SAM-PCA5472. B. *Anisoceras perarmatum* Pictet & Campiche. Lateral view of SAM-PCA3339, showing change of ornament on the body chamber. D. *Hamites duplicatus* Pictet & Campiche. Lateral view of SAM-PCA2955. F. *Hamites virgulatus* Brongniart. Lateral view of SAM-PCA3158, showing *venetianus*-type ribbing. G. *Mariella* (*Mariella*) *gresslyi* (Pictet & Campiche). SAM-PCA3133. H. *Hamites virgulatus* Brongniart. Lateral view of SAM-PCA2959, showing rather dense *subvirgulatus*-type ribbing. J-K. *Anisoceras phillipsi* sp. nov. Lateral and dorsal views of SAM-PCA 4799. B $\times 0,75$, other $\times 1$.

interpreted. Indeed, Sowerby's figure bears no great resemblance to the original and shows too many intercalated ribs both on the penultimate and final shafts, while the differentiation of the ribs on the final shaft is less prominent than is shown in Sowerby's drawing.

Anisoceras jacobi Breistroffer (nom. nov. pro *Anisoceras picteti* Spath (non Matheron) 1939: 554, pl. 59 (fig. 4), pl. 61 (fig. 8), pl. 63 (figs 3, 8), fig. 194) was diagnosed as follows: 'Like *A. armatum*, but more coarsely ornamented, with



Fig. 17. *Anisoceras armatum* (J. Sowerby). Sowerby's (1817, pl. 178) original figured specimen from the Upper Greensand of Roak, near Benson, Oxfordshire. Oxford University Museum K675a. $\times 1$.



Fig. 18. A-C. *Anisoceras armatum* (J. Sowerby), USNMNH 236952. $\times 1$.

the intermediate ribs (one, rarely two) as prominent as the main ribs that meet at the strong tubercles. Suture-line similar to that of *A. armatum*.'

These are the exact features which characterize the penultimate shaft of the holotype of the contemporaneous *A. armatum*, and the authors regard *A. jacobi* as a junior subjective synonym of *A. armatum*.

Anisoceras armatum and *A. perarmatum* are contemporaneous species which differ in that the latter generally lacks intercalatories between the

looped ribs in maturity, although there are intermediates between the two species, e.g. USNMNH 236952 (Fig. 18).

Spath (1939) noted the very close resemblance between *A. saussureanum* (Pictet) and *A. armatum* and considered immature growth stages indistinguishable. In maturity, *A. saussureanum* was said to differ by its distant tuberculation, with commonly two to three intercalatories between looped ribs, whilst coming from a lower level in the Albian. Spath (1939) appeared to place much weight, in his separation of the above two species, on the supposedly lower horizon of

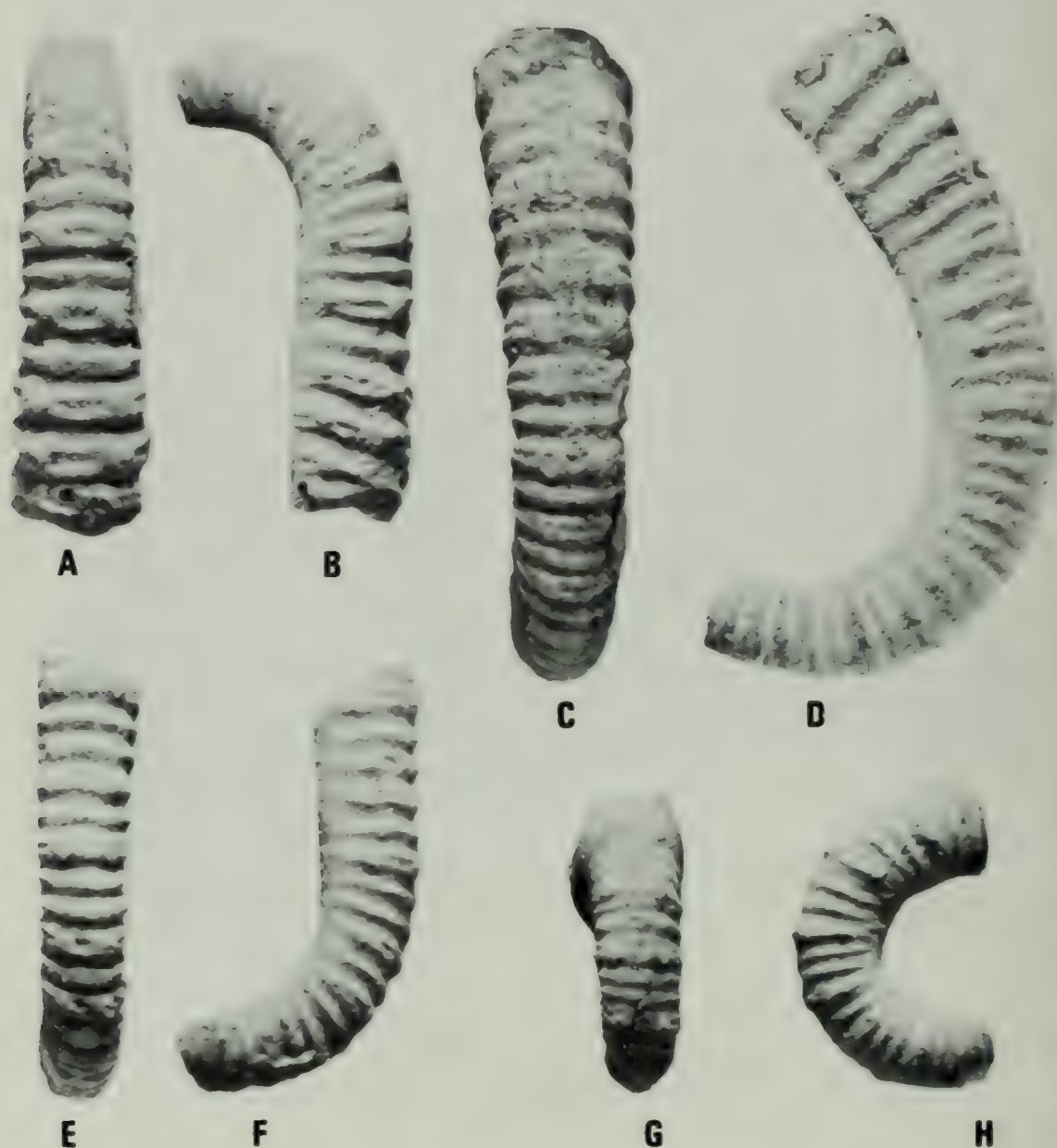


Fig. 19. *Anisoceras armatum* (J. Sowerby). A-B. USNMNH 236930. C-D. USNMNH 236936. E-F. USNMNH 236937. G-H. Doubtful juvenile, USNMNH 236939. $\times 1$.

A. saussureanum, although Breistroffer (1940, 1947) and Renz (1968) record it from the uppermost Albian of France and Switzerland respectively. Moreover, *A. saussureanum spinosum* (Haas) is recorded from the uppermost Albian of Angola and Mexico (*fide* Haas 1942). The holotype of *A. saussureanum spinosum* comes from the same locality as the Washburn collection and the authors have no hesitation in regarding it as a junior subjective synonym of *A. armatum*. However, Haas's identification clearly focuses on the difficulties of separating *A. armatum* and *A. saussureanum* and, in view of the fact that they are contemporary species in the uppermost Albian, they probably do not bear specific separation. However, until the type and topotype material of *A. saussureanum* are restudied with regard to their intraspecific variation, it seems preferable to retain these two well-known species separate.

Anisoceras tropicale (Meunier) (1887: 62, pl. 1 (fig. 5)) is based upon a very poorly preserved internal mould which was tentatively referred to *A. armatum* by Choffat (1905: 41) and Haas (1942: 191), although Spath (1939: 558) considered it closer to *A. pseudoelegans*. Meunier's specimen shows three fine intercalatories between looped ribs and, judging from the locality, a valley to the north of Lobito, is somewhat older than *A. armatum*. This is supported by the example of *A. armatum* figured by Haas (1942, fig. 29), which the authors would assign to *A. tropicale*; it occurs on the reverse side of the holotype of *Mortoniceras vokesi* (Haas), topotype material of which comes from the mid-Upper Albian zone of *Elobiceras elobiense* (Cooper 1978) at Lobito, in association with *Puzosia cuvervillei* (Meunier).

Anisoceras exoticum Spath (1939: 555, pl. 59 (fig. 7), pl. 60 (fig. 4), pl. 63 (fig. 2), fig. 195) differs from *A. armatum* in having four to six intercalatories between main ribs, with very feebly-developed dorsolateral tubercles. The ribbing of this species is also attenuated across the siphonal line.

In *Anisoceras oldhamianum* (Stoliczka) (1865: 135, pl. 83 (figs 1–4), pl. 92 (fig. 1)) all the ribs of the early growth stages are tuberculate and presumably looped, whilst on the straight shaft there is a fine, non-tuberculate rib separating looped ribs. The early whorls are coiled in a shallow, open helix.

Occurrence

Anisoceras armatum is at present known with certainty only from the uppermost Albian of southern England, France, Switzerland, Sardinia, Angola, Texas, and Mexico.

Anisoceras haasi sp. nov.

Figs 20–22

Idiohamites (?) indet. sp., Haas, 1942: 195, pl. 45 (fig. 6).

Idiohamites spiniger Haas (*non* J. Sowerby), 1942: 195, pl. 46 (fig. 4), fig. 31a–b.

Idiohamites indet. sp., Haas, 1942: 197, pl. 45 (fig. 7), fig. 31c.

Idiohamites aff. *subspinigero* Haas (*non* Spath), 1942: 197, pl. 46 (fig. 5), fig. 31d–e.

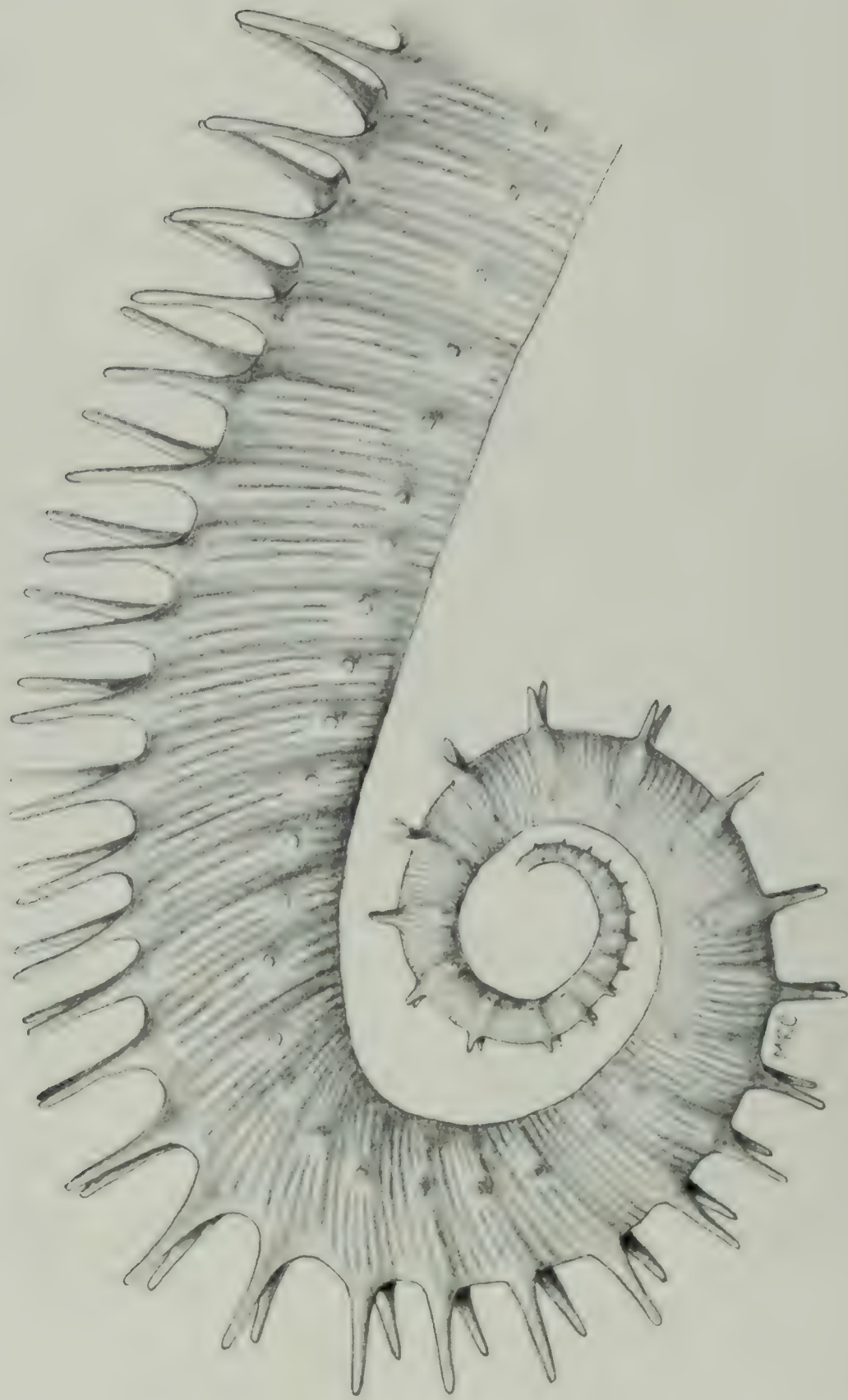


Fig. 20. *Anisoceras haasi* sp. nov. Reconstruction of early and middle growth stages. $\times 1$.



Fig. 21. *Anisoceras haasi* sp. nov. A-C. USNMNH 236923. D, F, H. USNMNH 236924. E, G. USNMNH 236922. I-J. USNMNH 236925. $\times 1$.

Material

Seven specimens, USNMNH 236922–7, all retaining recrystallized shell and all from Porto Amboim, together with a single crushed internal mould, SAM-PCA2952 from Praia-Egito.

Type material

USNMNH 236922 is designated holotype; the remaining specimens from Porto Amboim are paratypes.

Etymology

Named for Otto Haas, pioneer of ammonite studies on the Angola Cretaceous.

Diagnosis

A densely ribbed species of *Anisoceras* with 8–15 ribs in a distance equal to the whorl height; 2 or 3 ribs are looped from small, acute dorsolateral tubercles to prominent rounded bases of septate ventrolateral spines, commonly with 3–4 looped between tubercles across the venter; there are between 2 and 9 fine intercalatories separating looped ribs. Whorl section circular to elliptical, compressed.

Description

Up to 13 mm whorl-width: at this stage, the shell is coiled in a loose planispire, and has a slightly depressed to circular cross-section. Ornament comprises fine, slightly rursiradiate ribs, about as wide as the interspaces and effaced across the dorsum. There are periodic broad bulges which follow the course of the ribbing and are ornamented with very weak, pointed dorsolateral tubercles and the septate bases of large, prominent, ventrolateral spines. The fine ribs commonly arise in pairs from the dorsolateral tubercles and are joined by a third rib to meet the ventrolateral spine-base. Three to four ribs are looped across the venter connecting the ventrolateral spines. There are four to nine fine intercalated ribs between adjacent bulges.

14–16 mm whorl-width: beyond 13 mm whorl width, the shell begins to uncoil, developing an almost straight shaft. At the same time, the whorl section becomes slightly compressed ($W/H = 0,83–0,86$) and elliptical. The bulges become more regular with generally three in a distance equal to the whorl height, and commonly with two to three fine ribs separating adjacent bulges. Ribbing remains rursiradiate at this stage and the dorsolateral tubercles have migrated up flank to a low lateral position.

Discussion

The lectotype of *A. pseudoelegans* (Renz 1968, pl. 14 (fig. 12)) differs from the Angolan material in having a strongly compressed whorl section with flattened flanks and maximum width near the dorsolateral tubercles, whilst it is



Fig. 22. *Anisoceras haasi* sp. nov. Dorsal and lateral views of a slightly crushed composite internal mould, SAM-PCA2952, from Egito. $\times 1$.

more coarsely ribbed, with ribs arising in bundles from distinctly bullate dorso-lateral tubercles. Juveniles of *A. pseudoelegans* also appear to be much more coarsely ribbed than the present material (compare Renz 1968, pl. 14 (figs 10–11)).

According to Kennedy (1971: 12, pl. 3 (figs 12–13), pl. 4 (figs 1–3)), *Anisoceras plicatile* is a Middle Cenomanian species with 12 fine ribs in a distance equal to the whorl height, and a circular whorl section. 2 or 3 ribs are looped between the midlateral and ventrolateral tubercles and are separated by 1–3 non-tuberculate intercalatories. *Anisoceras plicatile* differs from the present material, therefore, in having much more swollen main ribs and a much more prominent lateral tubercle which is at the middle of the flank, not dorso-lateral as in *A. haasi*. The Angolan species also has more numerous, fine intercalatories, whilst the ribbing is not as coarse in maturity as it is in *A. plicatile* (compare Kennedy 1971, pl. 2 (fig. 12)).

Anisoceras bendirei (Adkins) (1920: 8, pl. 11 (fig. 1)) from the late Albian of Texas differs from the Angolan material in being much more coarsely ribbed, with the lateral tubercle higher on the flanks.

Anisoceras raynaudi (Boule, Lemoine & Thévenin 1907: 170, pl. 4 (figs 7–8), fig. 38) is a finely ribbed species in maturity, which differs from *A. haasi* in having fewer intercalatories (only 2–3) between looped ribs in the early growth stages, a more prominent dorsolateral tubercle and, judging from material from Catuane, southern Mozambique, in the South African Museum, Cape Town, in

having the early whorls coiled in an open helical spire up to 20 cm in height. It is also an earlier species (*orbignyi-varicosum* Subzones).

Anisoceras nanaense (von Hauer) (1861, pl. 1 (figs 11–12)) differs from the present species in lacking dorsolateral tubercles, and in having prorsiradiate ribs with only two to three intercalatories between tuberculate ribs.

Anisoceras arrogans (Giebel) (1852: 305) (nom. nov. pro *Hamites elegans* d'Orbigny (*non* Parkinson) 1842: 542, pl. 133 (figs 1–5)) can be distinguished from *A. haasi* in its lack of dorsolateral tubercles, with only two to four non-tuberculate intercalatories, and in the coarse, distant ribbing of the body chamber.

Occurrence

Anisoceras haasi sp. nov. is at present known only from the uppermost Albian of Angola.

Anisoceras phillipsi sp. nov.

Figs 16J–K, 23–24

Material

Eight fragments, SAM-PCA2974, 3179, 3183, 3211–3212, 3220 and 3222, all preserved as composite internal moulds, from Praia-Egito, and SAM-PCA4799 from the Quissama Ridge at Cabo Ledo.

Type material

The specimen illustrated as Figure 23, SAM-PCA3183 from Praia-Egito is designated as holotype. All other specimens cited above are paratypes.

Etymology

The species is named for Denis Phillips of the British Museum (Natural History) who, during many years, has given both authors invaluable assistance and advice in connection with their researches.

Diagnosis

A large species of *Anisoceras* with subrectangular, depressed to ovate whorl section in maturity. Prominent dorsolateral clavae give rise to two, occasionally only one, rursiradiate ribs which meet the well-developed ventrolateral clavae singly or in pairs. There are no intercalated ribs. Across the venter the ribs are looped or single.

Description

In the smallest example, SAM-PCA3179, the whorl section is elliptical, compressed, although it may have suffered lateral compaction. All the other larger fragments show a strongly depressed, subrectangular whorl section (Fig. 24) prior to the final hook, and an ovate whorl section afterwards.

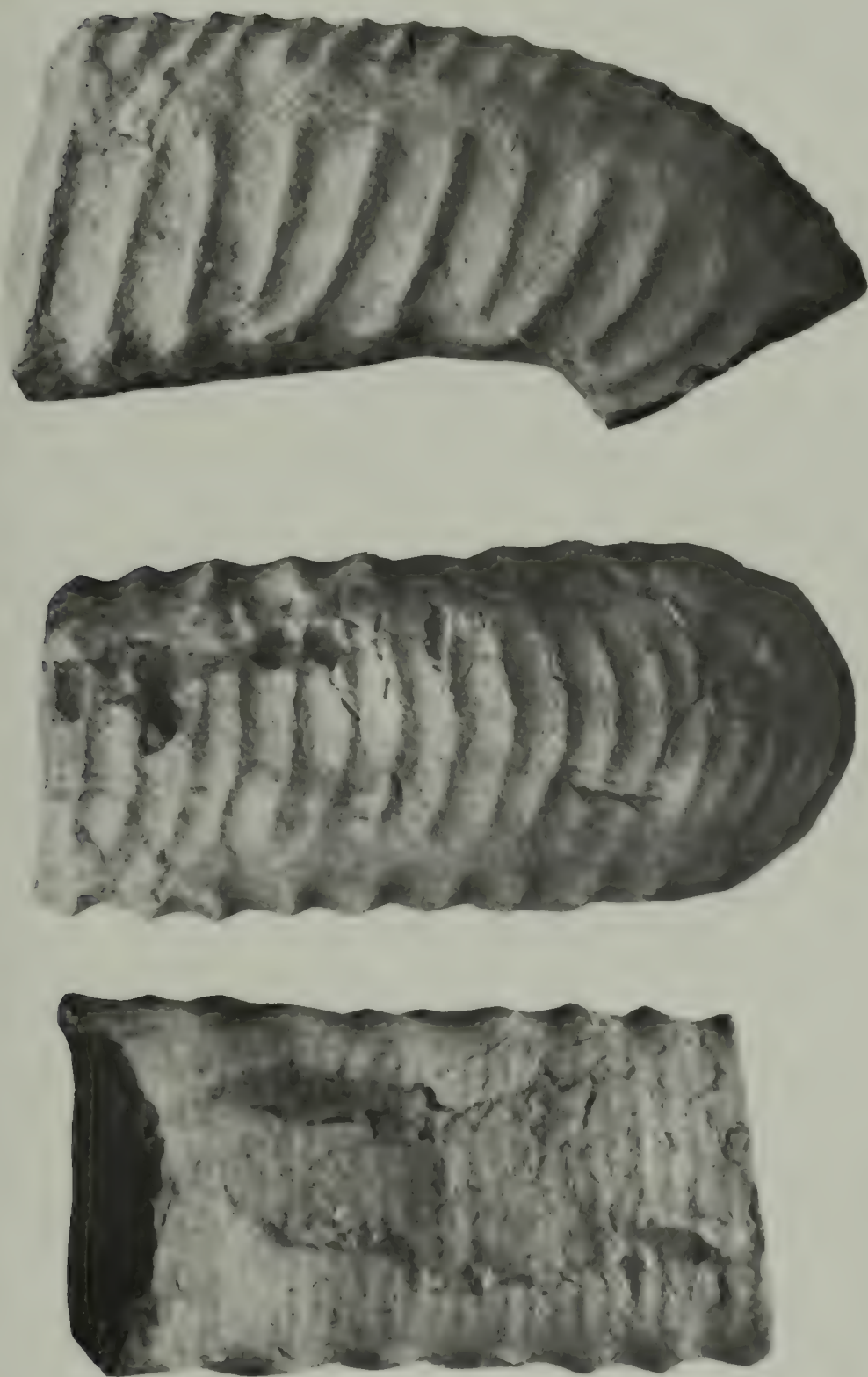


Fig. 23. *Anisoceras phillipsi* sp. nov. Dorsal, ventral and lateral views of the holotype, SAM-PCA3183, preserved as an internal mould. $\times 0,75$.

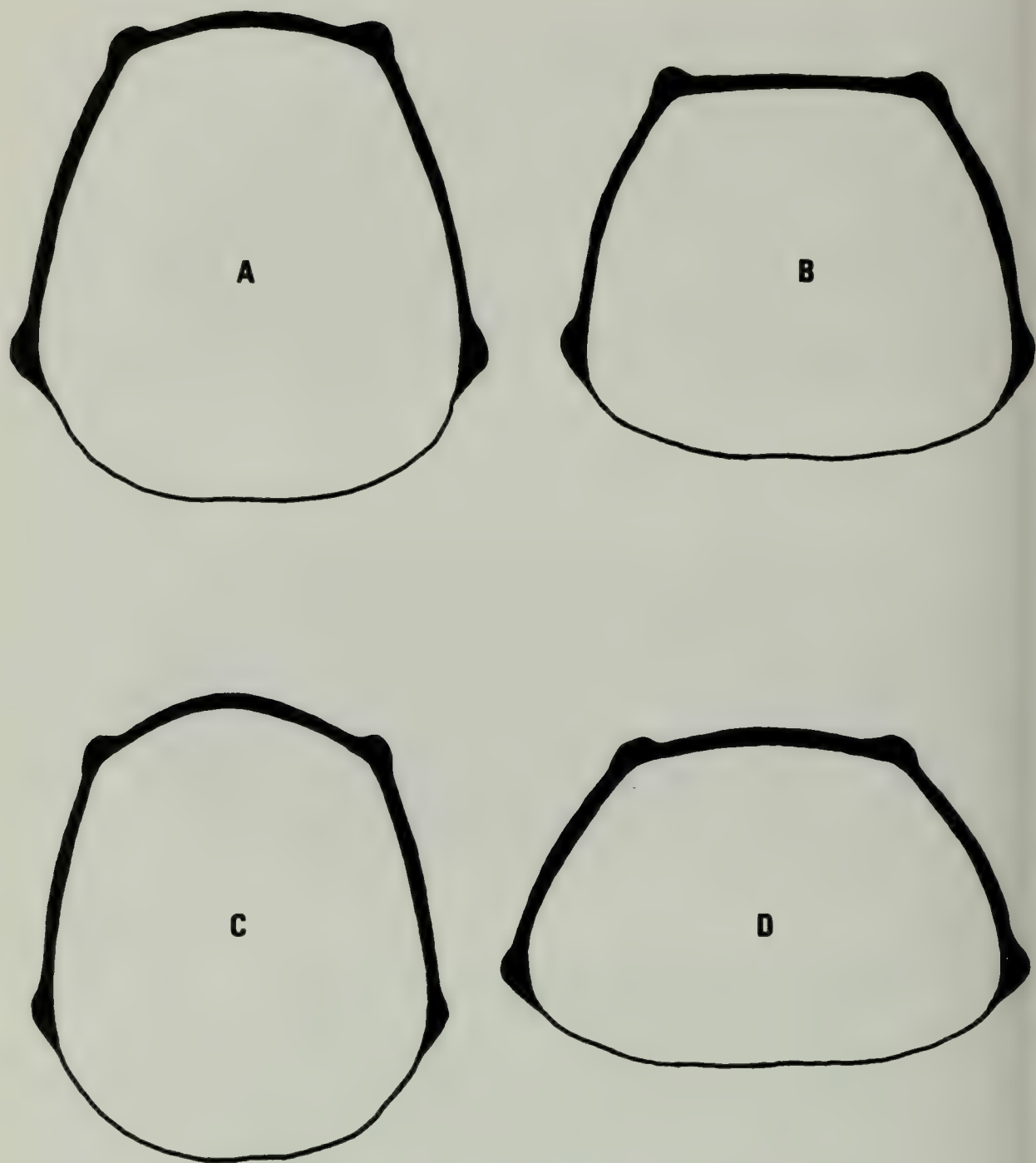


Fig. 24. *Anisoceras phillipsi* sp. nov. Whorl sections. A-B. SAM-PCA2974. C. SAM-PCA3183. D. SAM-PCA3222. $\times 1$.

On the dorsolateral shoulder, prominent clavae give rise to commonly two, sometimes only one, coarse, rursiradiate flank ribs which, on curved fragments, are strongly convex adorally. The flank ribs meet the well-developed ventrolateral clavi either singly or in pairs, with six to eight ribs in a distance equal to the whorl height. Across the venter, ribs are single or looped.

Discussion

The only species with which the present form may usefully be compared is *Anisoceras arrogans* (Giebel) (= *Anisoceras campichei* Spath 1942: 559, pl. 63 (figs 6–7), fig. 197) which differs in lacking the dorsolateral clavae and in the regular nature of its ribbing across the venter.

Occurrence

Anisoceras phillipsi sp. nov. is known only from the uppermost Albian of Angola.

Anisoceras cf. *arrogans* (Giebel, 1852)

Figs 25–26

Compare

Hamites elegans d'Orbigny (*non* Parkinson), 1842: 542, pl. 133 (figs 1–5).

Hamites arrogans Giebel, 1852: 305.

Anisoceras pseudoelegans Pictet & Campiche, 1861: pl. 50 (figs 6–7 only).

Anisoceras campichei Spath, 1926: 432; 1939: 559, fig. 197 only.

Metahamites (?) *arrogans* (Giebel) Spath, 1939: 559.

Anisoceras aff. *campichei* Spath, 1939: pl. 63 (figs 6–7).

Anisoceras arrogans (Giebel) Wiedmann & Dieni, 1968: 69, pl. 7 (fig. 10), pl. 8 (figs 5, 7, 11), figs 46–50.

Description

This species is known only from large fragments. In SAM-PCA3205, the whorl section is slightly compressed, subquadrate, but the remaining material shows some variation in this character.

Ornament comprises prominent, single flank ribs arising from weak umbilical tubercles and passing slightly prorsiradiate across the flanks to the bases of large, septate ventrolateral spines. Ribs are either single or looped across the venter, and the rib pattern is shown in Figure 26. There are six to seven flank ribs in a distance equal to the whorl height. Across the dorsum, fine ribs are looped between the weak dorsolateral tubercles, with generally an intercalated rib between pairs, so that there are about fifteen ribs across the dorsum per five dorsolateral tubercles.

Discussion

The present specimen is closest to *Anisoceras arrogans* (Giebel) (= *A. campichei* Spath, 1939: 559, fig. 197 only) from which it differs in its subquadrate whorl section, slightly prorsiradiate flank ribs, and the fact that all

ribs across the venter arise from ventrolateral tubercles. *Anisoceras arrogans* also does not show the peculiar zigzagging of the ribs across the venter (see Fig. 26) seen in the Angolan material. However, since *A. arrogans* and the present material represent different ontogenetic stages, the differences may not be as great as they first appear, and consequently the present material is identified as *A. cf. arrogans* (Giebel).

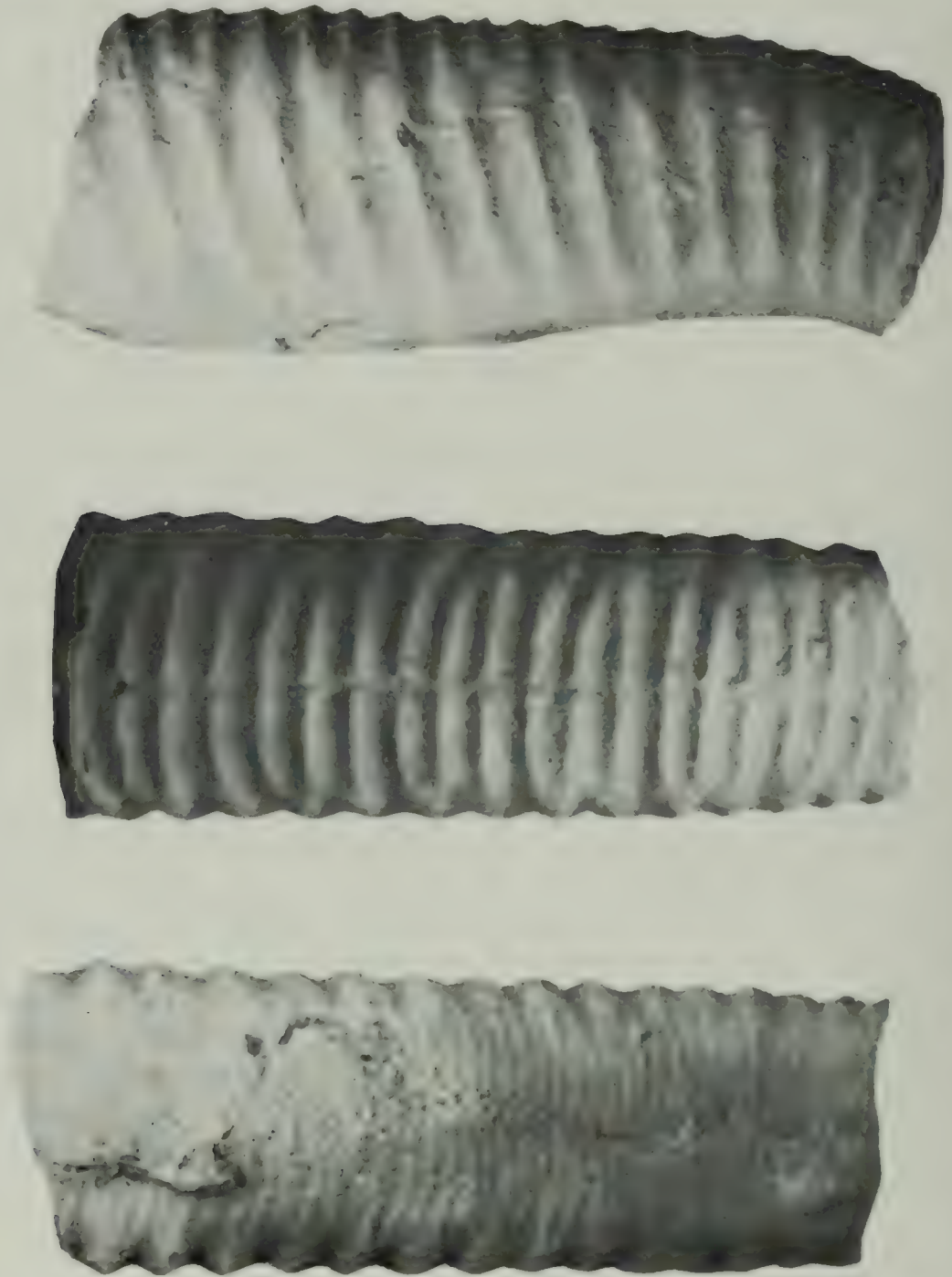


Fig. 25. *Anisoceras cf. arrogans* (Giebel). Dorsal, ventral and lateral views of SAM-PCA3205. $\times 0,75$.

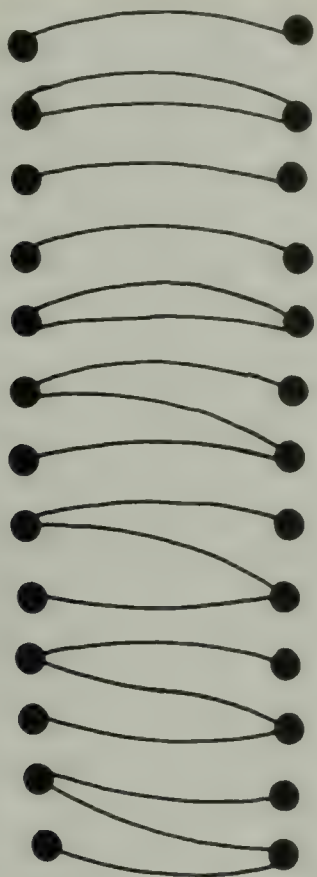


Fig. 26. *Anisoceras* cf. *arrogans* (Giebel). Schematic rib pattern across the venter of SAM-PCA3205. $\times 0,75$.

Anisoceras phillipsi sp. nov. differs from the present material in the possession of distinctly clavate dorsolateral tubercles, from which ribs frequently arise in pairs.

Occurrence

Anisoceras arrogans is known from the uppermost Albian of Switzerland, France and Sardinia, and may also be present in southern England and Angola.

Anisoceras aff. *exoticum* Spath, 1939

Fig. 27

Compare

Anisoceras saussureanum Pictet & Campiche (*non* Pictet), 1861: 118, pl. 1 (fig. 2).
Anisoceras exoticum Spath, 1939: 555, pl. 59 (fig. 7), pl. 60 (fig. 4), pl. 63 (fig. 2), fig. 195.

Material

A single specimen, SAM-PCA3174, preserved as a composite internal mould, from Praia-Egito.

Description

The specimen represents a slightly crushed fragment of a straight shaft in which the whorl section was originally probably almost circular. Ornament comprises slightly rursiradiate main ribs between which are three to seven fine, secondary ribs, the density of which increases adorally. The fragment lacks obvious tuberculation.



Fig. 27. *Anisoceras* aff. *exoticum* Spath. A body chamber fragment, SAM-PCA3174. $\times 0,75$.

Discussion

The specimen is a body chamber fragment and, since ornament frequently changes drastically on the body chamber of *Anisoceras*, reference to Spath's species is somewhat tentative.

Occurrence

Anisoceras exoticum is known from England, Switzerland, Sardinia, and possibly Angola.

Anisoceras aff. *subarcuatum* Spath, 1939

Fig. 28

Compare

Anisoceras subarcuatum Spath, 1939: 560, pl. 65 (fig. 1), pl. 66 (fig. 1), fig. 198.

Material

A single specimen, SAM-PCA3143, from the *dispar* Zone at Praia-Egito.

Description

A short fragment shows affinities with Spath's species and may belong here. The whorl section is slightly compressed, oval. Ornament comprises slightly rursiradiate, strengthened, simple main ribs which bifurcate or trifurcate across the dorsum and are ornamented with dorsolateral and ventrolateral tubercles. Between main ribs are two to three, slightly weaker, somewhat irregular secondary ribs, which occasionally bifurcate across the venter. All the secondary ribs lack tubercles.

Discussion

Body chamber fragments of *Anisoceras* are notoriously difficult to identify and hence full determination of the present specimen must await further material.



Fig. 28. *Anisoceras* aff. *subarcuatum* Spath. Ventral, lateral and dorsal views of SAM-PCA3143. $\times 0,75$.

Occurrence

Anisoceras subarcuatum is known with certainty only from the low Upper Albian (*varicosum* and *auritus* subzones) of southern England, but may also be present in the uppermost Albian of Angola.

Anisoceras aff. *spathi* (Wiedmann, 1962)

Fig. 29

Compare

Anisoceras subarcuatum Spath, 1939: 560, pl. 63 (fig. 5 only).

Idiohamites spathi Wiedmann, 1962a: 188.

Material

A single fragment, SAM-PCA3223, from the upper part of the *dispar* Zone at Praia-Egito, preserved as a composite internal mould.



Fig. 29. *Anisoceras* aff. *spathi* (Wiedmann). Ventral and lateral views of SAM-PCA3223. $\times 0,75$.

Description

The single fragment available represents part of the crozier. It has a compressed, elliptical whorl section with simple rursiradiate ribs. On the adoral portion of the fragment all ribs are relatively fine, of even strength, and lack tuberculation. On the adapical portion, every second rib is strengthened slightly and bears weak ventrolateral tubercles.

Discussion

The absence of lateral or dorsolateral tubercles led Wiedmann (1962a) to assign the present species to *Idiohamites*. However, the holotype is a body-chamber fragment which merely shows the radical change in ornament on the body chamber displayed by many *Anisoceras* species.

Occurrence

Anisoceras spathi is known from the low Upper Albian of southern England and Spain, and may be present in the *dispar* Zone of Angola.

Anisoceras sp. indet.

Fig. 14F

Material

A single, crushed fragment, SAM-PCA3220, from Praia-Egito, preserved as a composite internal mould.

Description

Only the greater part of one flank, one row of ventrolateral tubercles and much of the venter of the specimen concerned is preserved.

Rather fine (?looped) ribs on the flanks are slightly narrower than the interspaces, with at least 10 in a distance equal to the whorl height. The flank ribs join the ventrolateral clavi in pairs whereas, across the venter, the ventrolateral tubercles are connected by 2-3 ribs so that for 16 flank ribs, there are 20 ribs across the venter. The whorl section gives the appearance of having been strongly depressed.

Discussion

The specimen under discussion is too poorly preserved for specific identification, but may be regarded as belonging to the *plicatile-haasi* plexus.

Occurrence

Upper Albian, *dispar* Zone, Praia-Egito.

Genus *Idiohamites* Spath, 1925Type species *Hamites tuberculatus* J. Sowerby, 1818*Discussion*

Wiedmann (1962a) separated *Idiohamites* from *Anisoceras* because the former was considered to have the early whorls coiled in a helix, whereas in *Anisoceras* the juvenile whorls were considered to be planispirally coiled. The differences are not, however, so clear cut, since *Anisoceras* of the type referred to *A. raynaudi* (Boule, Lemoine & Thévenin) by Förster (1975) (= *Anisoceras saussureanum quadrifasciatum* Klinger) from the low Upper Albian of Catuane, Mozambique, and now in the South African Museum, show the early whorls to be coiled in an open helix up to 20 cm high. The straight final shafts of this species are figured by Förster (1975, pl. 4 (fig. 8)). Moreover, Matsumoto (1959, pl. 28 (fig. 1), pl. 29 (fig. 2)) has also figured an *Anisoceras* in which the early growth stages are helically coiled.

Nor is the presence or absence of lateral tubercles a diagnostic feature since some *Anisoceras*, e.g. *A. auberti* (Pervinquière) and *A. gracile* Renz, lack them. Moreover, Renz (1968) has recently figured a number of specimens which he considers transitional between *Idiohamites* and *Anisoceras* in this respect (cf. pl. 12 (figs 7–8), pl. 13 (figs 3, 6)). In addition both genera show a suture line with a fairly shallow, bifid external lobe (E), an asymmetrically bifid first lateral saddle (E/L), a bifid first lateral lobe (L) which is deeper than the external lobe, and a second lateral saddle (L/U) which is bifid, and a bifid second lateral lobe (U) which is almost as deep as the first. Clearly the two genera are very closely related although, at present, the typically smaller size, almost complete absence at any growth stage of looped flank ribs, and the helically coiled juvenile whorls, are considered to be sufficient for the generic separation of *Idiohamites* from *Anisoceras*.

Idiohamites dorsetensis Spath, 1926

Figs 30, 31G

Anisoceras alternatus Pictet & Campiche (*non* Mantell), 1861: 71, pl. 51 (figs 1, 3–4).

Idiohamites dorsetensis Spath, 1926b: 432; 1939: 596, pl. 62 (figs 2–3), pl. 63 (figs 1, 9, 15), pl. 65 (fig. 2), fig. 215. Renz, 1968: 70, pl. 11 (figs 39–40), pl. 12 (figs 3–4), figs 25a–d, f, 26a–d.

? *Idiohamites* aff. *turgidus robustus* Spath, Renz, 1968: 72, pl. 11 (figs 33–37), figs 25k–l, 26f–h.

? *Idiohamites elegantulus laticostatus* Renz, 1968: 73, pl. 11 (figs 38, 41–42), pl. 12 (figs 1–2), figs 25m, 26i–m.

Material

Three specimens in the South African Museum, SAM-PCA4803 and two unnumbered fragments, retaining recrystallized test, together with USNMNH 236951, preserved as a composite internal mould from Porto Amboim, and a single specimen from Cabo Ledo, SAM-PCA5469.



Fig. 30. A–D. *Idiohamites dorsetensis* Spath. A–B. Ventral and lateral views of SAM-PCA4803. C–D. Ventral and lateral views of SAM-PCA5469. $\times 1$.

Description

All the fragments show the shell to be loosely coiled in a single plane, with an elliptical, compressed whorl section. Ornament comprises simple, strong, slightly prorsiradiate ribs, of which there are four to five in a distance equal to the whorl height. Every second or third (or occasionally adjacent) rib bears very small, sharp, pointed lateral tubercles and more prominent ventrolateral spines. At small growth stages, tubercles are connected across the venter by simple ribs but, on the mature body chamber, they may be weakly looped.

Discussion

Until populations of individuals are available for study, the differences between several named species of *Idiohamites* appear suspiciously small. The authors assign their material to *I. dorsetensis* because of the very close similarities to the types, and because it is the oldest available name for material of this age.

Occurrence

Idiohamites dorsetensis is known from the uppermost Albian of southern England, France, Switzerland and Angola.

Idiohamites cf. *elegantulus* Spath, 1939

Fig. 31A–D

Compare

Idiohamites elegantulus Spath, 1939: 599, fig. 216.

Material

One specimen, USNMNH 236950, a composite internal mould from Porto Amboim.

Discussion

The specimen consists of a body chamber hook with a maximum whorl height of 12 mm. There are six fine prorsiradiate ribs in a distance equal to the whorl height, the majority bearing ventral tubercles, suggesting reference to Spath's species.

Occurrence

Stoliczkaia dispar Zone of England, and possibly Angola.

Idiohamites pygmaeus sp. nov.

Fig. 31J–N

Material

Eight specimens, USNMNH 236942–49, all retaining recrystallized shell and all from Porto Amboim.

Type material

USNMNH 236942, a complete adult, is designated holotype; the remaining specimens are paratypes.

Etymology

From the Latin adjective *pygmaeus*, pygmy-like, dwarfish; derived from the Greek *pygmaios*. The *pygmaioi* were a fabulous dwarfish race of antiquity, especially in Africa; at war with the cranes, they were constantly defeated (Pliny).



Fig. 31. A-D. *Idiohamites* cf. *elegantulus* Spath. A-B. USNMNH 236948. C-D. USNMNH 236938. E-F. *Mariella* (*Mariella*) *circumtaeniatus* (Kossmat), USNMNH 236958. G. *Idiohamites* cf. *dorsetensis* Spath, USNMNH 236951. H-I. *Borissiakoceras* sp. nov.? aff. *reymonti* (Brunnschweiler), USNMNH 236980. J-N. *Idiohamites* *pygmaeus* sp. nov. J-L. USNMNH 236942. M-N. USNMNH 236943. $\times 1$.

Diagnosis

A very small *Idiohamites* with a known maximum length of only 52 mm, characterized by helicoid early whorls with three quadrituberculate rursiradiate ribs in a distance equal to the whorl height, a straight shaft with four prorsiradiate ribs in a distance equal to the whorl height and ribbing tending to be rectiradiate at the aperture.

Description

Shell small, initially coiled in a low, open helical spire, straightening in maturity before recurving on the body chamber to form a crozier.

Earliest whorls ornamented with rather robust ribs, narrower than the interspaces and with three in a distance equal to the whorl height, which cross the venter obliquely so that the four rows of tubercles on the main ribs are asymmetrically arranged. There is a regular alternation of tuberculate and non-tuberculate ribs, which, at this stage, are slightly rursiradiate. On the first straight shaft, which commences at a whorl height of 6 mm, the ribbing becomes prorsiradiate, with still only three ribs in a distance equal to the intercostal whorl height. With the uncoiling of the shell, the tuberculation is no longer asymmetrical and main ribs are ornamented with small pointed dorsolateral and ventrolateral tubercles. The rib direction changes to rectiradiate on the final shaft. In maturity, the intercostal whorl section is oval, depressed, although it is almost circular at small diameters.

Discussion

This species is characterized by its small size at maturity. *Idiohamites dorsetensis* is adult at much larger diameters, with a slightly compressed whorl section, and closer ribbing (four to six in a distance equal to the whorl height). *Idiohamites elegantulus* is even more densely ribbed (seven in a distance equal to the whorl height), also with a compressed whorl section. *Idiohamites recticostatus* Renz is a much larger species with an almost circular whorl section and four rectiradiate ribs in a distance equal to the whorl height. It closely approaches the present material, but its very much larger size (septate at 23 mm whorl height) is distinctive.

Occurrence

Uppermost Albian of Angola only.

Family **Hamitidae** Hyatt, 1900

Genus *Hamites* Parkinson, 1811

Type species *Hamites attenuatus* J. Sowerby, 1814

Discussion

Recent discussions of the family are to be found in Wiedmann & Dieni (1968) and Klinger (1976), and further discussion on the material available here is unnecessary.

Hamites virgulatus Brongniart, 1822

Figs 16F, H, 32B–C

Hamites virgulatus Brongniart (in Cuvier & Brongniart), 1822: pl. 0 (fig. 6).*Hamites* (*Stomohamites*) *virgulatus* (Brongniart?) Pictet & Campiche, Spath, 1941: 635, pl. 71 (figs 7–10), pl. 72 (fig. 11), fig. 230 (with synonymy). Renz, 1968: 65, pl. 11 (figs 9–11), fig. 23b–d (with synonymy).*Hamites* (*Stomohamites*) *subvirgulatus* Spath, 1941: 645, fig. 234. Renz, 1968: 66, pl. 11 (figs 13–14), figs 23e, 24a (with synonymy).*Stomohamites brongniarti* Breistroffer, 1947: 77.*Hamites* (*Hamites*) *virgulatus* Brongniart, Wiedmann & Dieni, 1968: 53, pl. 5 (figs 1–2, 10), pl. 7 (figs 1–2), figs 21–27. Klinger, 1976: 60, pl. 23 (figs 4–5, 8), figs 8 l,n–o, 11i (with synonymy).*Hamites venetzius* Pictet (in Pictet & Roux), 1847: 134, pl. 14 (fig. 6).*Hamites* (*Stomohamites*) *venetzius* Pictet, Spath, 1941: 638, pl. 71 (figs 11–13), fig. 231. Renz, 1968: 67, pl. 11 (figs 15–16), figs 23f, 24b (with synonymy).*Material*

Ten composite internal moulds, SAM-PCA2959, 2963–64, 2966, 2971, 3118, 3157–58, and 3371 from the upper part of the *dispar* Zone at Praia-Egito, three fragments retaining recrystallized tests from Porto Amboim, USNMNH 236955–7, and SAM-PCA4603 from Cabo Ledo.

Description

The whorl section is elliptical compressed, with three to six prorsiradiate ribs in a distance equal to the whorl height. The ribs are effaced across the dorsum.

Discussion

The writers follow Wiedmann & Dieni (1968) in regarding *H. brongniarti*, *H. venetzius*, and *H. subvirgulatus* as synonyms of *H. virgulatus*, although there may be some justification for retaining *venetzius* at the varietal level for those variants in which the ribs are as thick as, or thicker than, the interspaces.

Hamites duplicatus Pictet & Campiche, 1861

Figs 16D, 32A

Hamites virgulatus Pictet (*non* Brongniart) (in Pictet & Roux), 1847: 391, pl. 14 (figs 7, 9 only).*Hamites duplicatus* Pictet & Campiche, 1861: 98.*Hamites* (*Stomohamites*) *duplicatus* Pictet & Campiche, Spath, 1941: 640, pl. 72 (figs 12–16), fig. 232. Renz, 1968: 68, pl. 11 (figs 19–21), fig. 23h–k.*Material*

A single composite internal mould from Praia-Egito, SAM-PCA2955.

Description

The whorl section is oval, compressed, with a somewhat flattened dorsum. Ornament comprises fine, rursiradiate ribs, seven in a distance equal to the whorl height, which are very weak across the dorsum.

Discussion

The writers are not convinced by Wiedmann & Dieni's (1968) argument for the inclusion of *H. duplicatus* in the synonymy of *H. virgulatus* and, for the present, maintain it as distinct.

Occurrence

Hamites duplicatus is known from the Upper Albian of England, France, Switzerland, and Angola.

Superfamily TURRILITACEAE Meek, 1876

Family Turrilitidae Meek, 1876

Subfamily Turrilitinae Meek, 1876

Genus *Mariella* Nowak, 1916Type species *Turrilites bergeri* Brongniart, 1822*Discussion*

Kennedy (1971) and Klinger & Kennedy (1978) have recently provided a comprehensive discussion of the taxonomic standing of *Mariella*, including in it three subgenera, viz. *M. (Mariella)*, *M. (Plesioturrilites)* and *M. (Wintonia)*.

As noted by Clark (1965: 49), however, *M. (Wintonia)* and *M. (Plesioturrilites)* differ only in that the former has an early, straight shaft which then passes into the helical coiling of *M. (Plesioturrilites)*, although specimens of *M. (Wintonia) graysonensis* (Adkins), the only known species, cannot be distinguished from *M. (Plesioturrilites) bosquensis* (Adkins) in the absence of this straight shaft. Klinger & Kennedy (1978) suggest the 'shaft' is an artefact of preservation and treat *Plesioturrilites* as a synonym of *Wintonia*.

Mariella (Mariella) circumtaeniatus (Kossmat, 1895)

Figs 31E–F, 39H

Turrilites gresslyi Stoliczka (*non* Pictet & Campiche), 1865: 186, pl. 87 (figs 1–5, ? *non* 2).

Turrilites circumtaeniatus Kossmat, 1895: 141, pl. 18 (figs 4–5); Boule, Lemoine & Thévenin, 1907: 57, pl. 13 (fig. 4).

Non Turrilites circumtaeniatus Scott (*non* Kossmat), 1926: 145, pl. 1 (figs 10–11) (= *M. worthensis*).

Paraturrilites aff. *circumtaeniatus* (Kossmat) Collignon, 1963: 46, pl. 258 (fig. 1120).

Non Turrilites circumtaeniatus Kossmat, Woods, 1917: 11, pl. 5 (figs 2–3) (= *M. thomsoni* Henderson).

Material

A single specimen USNMNH 236958, with recrystallized shell preserved, from Porto Amboim.

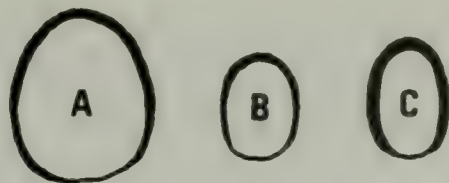


Fig. 32. A. *Hamites duplicatus* Pictet & Campiche. Whorl section of SAM-PCA2955. B-C. *Hamites virgulatus* Brongniart. Whorl sections. B. SAM-PCA2959. C. SAM-PCA3158. $\times 1$.

Description

Coiling sinistral, with a very acute apical angle (approximately 20°). Flanks rounded intercostally, with two rows of prominent, rounded tubercles and a third hidden in the spiral seam. There are nine to eleven tubercles per half-whorl situated on very weak, slightly oblique ribs. The upper row of tubercles is situated slightly above mid-flank, and the central row midway between the upper row and the lower spiral suture. Ribbing is conspicuous only on the area between the upper row of tubercles and the upper spiral suture, where rather fine ribs commonly connect in pairs to the upper row of tubercles, frequently with an intercalated rib between tubercles.

Discussion

Amongst contemporaneous species of *Mariella*, *M. (M.) cantabrigiensis* (Jukes-Browne) (Spath 1937: 518, pl. 57 (fig. 36), pl. 58 (figs 1-2), figs 181a-b, 182d-e) approaches the present species most closely. It differs in its much larger spiral angle (30° or more) and in lacking the fine looped ribs on the upper, outer face of the whorls.

M. (Mariella) nobilis (Jukes-Browne) (Spath 1937: 520, pl. 58 (figs 10-11), fig. 182) differs in having more prominent single ribs and subdued tuberculation.

M. (Mariella) bergeri (Brongniart) (1822: 395, pl. 7 (fig. 3)), of which *M. (M.) miliaris* (Pictet & Campiche) (1861: 136, pl. 51 (fig. 5)) may be only an extreme variant, has four rows of tubercles exposed on the outer face of the whorls.

M. (Mariella) dubourdieui (Collignon) (1963: 46, pl. 285 (fig. 1121)) resembles *M. (M.) circumtaeniatus* in the possession of looped ribs, but also has four rows of tubercles exposed on the outer face of the whorls.

M. (Mariella) worthensis (Adkins & Winton) (1920: 44, pl. 7 (figs 10-11, 13)) from the uppermost Albian Pawpaw Formation of Texas, closely resembles *M. (M.) circumtaeniatus*, but appears to lack the fine looped ribs of Kossmat's species, as does *M. (M.) hillyi* (Dubourdieu) (1953: 46, pl. 4 (figs 1-3)).

Occurrence

This species is known from the uppermost Albian of India, Madagascar, Zululand, Angola, and New Zealand.

Mariella (Mariella) nobilis (Jukes-Browne, 1877)

Fig. 33A–B

Turrilites intermedius Pictet & Campiche, 1861: 127, pl. 57 (fig. 15 only).*Turrilites escherianus* Pictet & Campiche (*non* Pictet), 1861: 130, pl. 56 (figs 6–8 only).*Turrilites nobilis* Jukes-Browne, 1877: 493, pl. 21 (fig. 1).*Mariella nobilis* (Jukes-Browne) Breistroffer (*in* Besairie), 1936: 147. Spath, 1937: 520, pl. 58 (figs 10–11), fig. 182a–c. Breistroffer, 1940: 147. Clark, 1965: 40, pl. 10 (figs 2–4), pl. 11 (figs 4–5). Renz, 1968: 89, pl. 17 (figs 28, 40), figs 31l, 32k.*Mariella nobilis* var. *cruciana* Breistroffer (*in* Besairie), 1936: 148. Spath, 1937: 521. Breistroffer, 1940: 148. Renz, 1968: 90, pl. 17 (fig. 34), figs 31b, 32d.*Mariella* aff. *nobilis* (Jukes-Browne) Spath, 1937: 520, pl. 58 (fig. 21).*Paraturrilites nobilis* (Jukes-Browne) Breistroffer, 1947: 60; 1953: 1350.*Paraturrilites nobilis* var. *cruciana* (Breistroffer) Breistroffer, 1947: 60.*Paraturrilites nobilis* var. *brownei* Breistroffer, 1947: 96.*Mariella nobilis brownei* (Breistroffer) Renz, 1968: 90, pl. 17 (figs 35–36, 38–39), figs 31i, 32e.*Material*

Two specimens, SAM-6531 (from an unknown location on the Angolan littoral), and a single fragment in the Washburn collection, USNMNH 237019 from Porto Amboim.

Description

These two fragments of *M. (Mariella)* bear prominent oblique ribs, narrower than the interspaces, estimated at totalling twenty-six per whorl. They are ornamented by three rows of weak tubercles; the tubercles of the adoral row are weakly clavate, whereas those of the other two rows are weakly rounded.

Discussion

M. (Mariella) nobilis var. *cruciana* Breistroffer (*in* Besairie 1936: 148) was separated from the typical form by its denser ribbing (30 ribs per whorl, as against 26–28) and more prominent tubercles. *M. (Mariella) nobilis* var. *brownei* Breistroffer (1947: 96) was distinguished by its sparser ribbing (24–26 per whorl) and weaker tuberculation.

As noted by Spath (1937: 521), *M. (Mariella) escheriana* (Pictet) (*in* Pictet & Roux 1847: 154, pl. 15 (fig. 11)) closely resembles the present species and there even appear to be intermediates. Pictet's species was distinguished by its denser ribbing (35–40 ribs per whorl), and flattened flanks with only two rows of tubercles.

The closest species to *M. (M.) nobilis* is *M. (M.) cantabrigiensis* (Jukes-Browne) (Spath 1937: 518, pl. 57 (fig. 36), pl. 58 (figs 1–2), figs 181a–b, 182d–e) from the late Albian of western Europe. Not only are they strictly contemporaneous, but Spath (1937: 519) also admits to the presence of intermediates. Typically, however, it differs in its sparser ribbing and more prominent tubercles.

M. (Mariella) worthensis (Adkins & Winton) (1920: 44, pl. 7 (figs 10–11, 13)) is very close to *M. (M.) nobilis* but is generally more coarsely ribbed (14–28 ribs per whorl) with four rows of tubercles per whorl.

M. (Mariella) gresslyi, *M. (M.) cantabrigiensis*, *M. (M.) nobilis*, *M. (M.) escheriana*, *M. (M.) worthensis* and *M. (M.) hillyi* are a contemporaneous group of very closely allied species whose intraspecific variation clearly needs documenting before the true taxonomic status of the species involved can be resolved.

Occurrence

M. (Mariella) nobilis is known only from the upper Upper Albian of southern England, Texas, and Angola.



Fig. 33. A-B. *Mariella (Mariella) nobilis* (Jukes-Browne), SAM-6531. C-D. *Puzosia* (*Puzosia*) sp., SAM-6407. $\times 1$.

Mariella gresslyi (Pictet & Campiche, 1861)

Fig. 16G

Turrilites gresslyi Pictet & Campiche, 1861: 132, pl. 57 (figs 11-13). Neumayr, 1875a: 901. Renevier, 1890: 339. Pervinquier, 1910: 54. Böse, 1923: 147. Diener, 1925: 83. Collignon, 1929: 65, pl. 1 (fig. 15).

Turrilitoides (?) *gresslyi* (Pictet & Campiche) Breistroffer, 1936: 65.

Mariella gresslyi (Pictet & Campiche) Spath, 1937: 516, pl. 58 (figs 3-4), fig. 180. Breistroffer, 1940: 149. Renz, 1968: 89, pl. 17 (figs 30a-b, 32-33), figs 31c, 32a-b.

Paraturrilites gresslyi (Pictet & Campiche) Breistroffer, 1947: 60. Collignon, 1963: 47, pl. 258 (fig. 1122).

? *Turrilites gresslyi* Pictet & Campiche, Boule, Lemoine & Thévenin, 1907: 39, pl. 6 (fig. 2).

Mariella gresslyi bifurcata Renz, 1968: 89, pl. 17 (fig. 42a-b), figs 31e, 32c.

? *Turrilites cantabrigiensis* Jukes-Browne, 1877: 493.

? *Mariella cantabrigiensis* (Jukes-Browne) Spath, 1937: 518, pl. 57 (fig. 36), pl. 58 (figs 1-2), figs 181a-b, 182d-e.

Material

A single specimen, SAM-PCA3133, from low down in the coastal cliffs immediately north of the estuary at Praia-Egito, and thus from a level below the main *Stoliczkaia* occurrence.

Description

The specimen is rather poorly preserved, but retains recrystallized test. The shell is sinistrally coiled, with a moderately large apical angle. The outer faces of the whorls are gently convex intercostally, and angular, polygonal costally. Three rows of tubercles are visible on rather oblique ribs. The upper row of tubercles are conical whereas the middle row is distinctly clavate. The nature of the tubercles of the lower row was difficult to discern, but they, too, appear to be clavate.

Discussion

The features of the present specimen are those of *M. gresslyi* and the authors have no hesitation in assigning the Angolan example to this species.

Mariella cantabrigiensis (Jukes-Browne) (Spath, 1937: 518, pl. 57 (fig. 36), pl. 58 (figs 1–2), figs 180h, 181a–b, 182d–e) closely approaches *M. gresslyi*, but was said to differ in having all tubercles rounded, whereas the lower two rows are clavate in *M. gresslyi*. However, the two species are strictly contemporaneous and occur side by side, whilst Spath (1937) admits to transitions between the two. Population studies may show *M. cantabrigiensis* to be an intraspecific variant of *M. gresslyi*.

Mariella gresslyi bifurcata Renz (1968: 89, pl. 17 (fig. 42), figs 31e, 32c) is based on a single specimen which shows the ribs on the base of the spire bifurcating from the lowest (adoral) row of tubercles.

Mariella nobilis (Jukes-Browne) (Spath 1937: 520, pl. 58 (figs 10–11), figs 181c, 182a–c) differs from the present species in having very subdued tubercles, with ribs dominant.

Occurrence

Mariella gresslyi is currently known from southern England, France, Switzerland, Algeria, Angola, Zululand, and Madagascar.

Mariella cf. *oehlerti* (Pervinqui re, 1910)

Figs 3H, 34

Compare

Turrilites gresslyi Boule, Lemoine & Th venin (non Pictet & Campiche), 1907: 57, pl. 13 (fig. 2). Collignon, 1929: 65, pl. 6 (fig. 15).

? *Turrilites* cf. *gresslyi* Spath (non Pictet & Campiche), 1921: 289.

Turrilites oehlerti Pervinquière, 1910: 53, pl. 5 (figs 14–17). Collignon, 1929: 65, pl. 6 (figs 16–17); 1964: 15, pl. 320 (figs 1398–1399).

? *Mariella malgachensis* Breistroffer, 1940: 79.

? *Turrilites bergeri* Choffat (*non* Brongniart), 1903: 15, pl. 1 (figs 4–6).

? *Mariella bergeri* var. *conduciensis* Breistroffer, 1940: 149.

Mariella (*Mariella*) *oehlerti* (Pervinquière), Förster 1975: 190, pl. 7 (figs 7–8), fig. 52. Klinger & Kennedy 1978: 31, pl. 3 (fig. E), pl. 4 (fig. E), pl. 6 (figs H, N), pl. 7 (fig. G), pl. 8 (figs G–H), figs 1a–b, 7b, d, 8g.

Material

A single composite internal mould, SAM-PCA4798, from the Quissama Ridge at Cabo Ledo.



Fig. 34. *Mariella* (*Mariella*) cf. *oehlerti* (Pervinquière), SAM-PCA4798. $\times 1$.

Description

The shell is a high-spired, sinistrally-coiled turrilite, with a spiral angle of about 22° . The whorls are just touching with the outer face gently convex, and somewhat flattened. The adapical shoulder is abrupt and subangular (Fig. 3H) whilst the adoral shoulder is evenly rounded. The outer face is ornamented with

four rows of prominent tubercles arranged on weak, oblique ribs, of which there are about thirty per whorl. The upper row of tubercles is the most prominent, and they are slightly bullate and situated slightly above mid-whorl. The tubercles of the two middle rows are conical and are separated by a weak spiral groove. The tubercles of the lower row are the smallest and are situated in the whorl seam. On the adoral face of the final whorl there are prominent ribs. The spacing of the tubercles is subequal on the penultimate whorl of the present specimen, but on the final whorl the middle two rows are distinctly closer together than the others.

Discussion

At present the species *M. gresslyi*—*M. cantabrigiensis*—*M. oehlerti*—*M. circumtaeniatus* are not well differentiated.

Mariella gresslyi (Pictet & Campiche) (1861: 132, pl. 57 (figs 11–13)) is typically an uppermost Albian species which differs from the present form and *M. oehlerti* in that the rows of tubercles are typically clavate. However, Spath (1937: 519) records passage form between *M. gresslyi* and the contemporaneous *M. cantabrigiensis* (Jukes-Browne) (Spath 1937: 518, pl. 51 (fig. 36), pl. 58 (figs 1–2)), the latter distinguished from Pictet & Campiche's species in having rounded tubercles of equal size, and thus very close to *M. oehlerti* and the Angolan material. Since, however, the present specimen is much larger than known material of *M. gresslyi* and *M. cantabrigiensis*, differences may be due to a comparison of different ontogenetic stages. Clearly, however, this problem cannot be resolved in the present paper.

Mariella circumtaeniatus has only three rows of tubercles, generally with conspicuous looping of the ribs on the adapical shoulder of the whorls.

Mariella dorsetensis (Spath) (= *Turrilites bergeri* Sharpe (*non* Brongniart) 1857: 65, pl. 26 (fig. 11 only)) differs from the present material in having fewer ribs per whorl and in having the third and fourth (adoral) rows of tubercles approximated, whilst ribs are absent on the base of the spire.

Mariella gallienii (Boule, Lemoine & Thévenin) (1906: 60, pl. 14 (figs 5–6)) differs from the present specimen in that the tubercles of the four rows are distinctly bullate.

Occurrence

Mariella oehlerti is known from the Lower Cenomanian of Algeria, Madagascar, Mozambique, Zululand, and possibly Japan, and possibly the uppermost Albian of Angola and Switzerland.

Suborder AMMONITINA Hyatt, 1889

Superfamily HOPLITACEAE Douvillé, 1890

Family **Desmoceratidae** Zittel, 1895

Subfamily Puzosiinae Spath, 1922

Genus *Puzosia* Bayle, 1878

Subgenus *Puzosia* Bayle, 1878

Type species *Ammonites planulatus* J. de C. Sowerby, 1827

Puzosia (Puzosia) sp.

Fig. 33C–D

Material

A single crushed specimen, SAM–6407, retaining recrystallized shell, from Porto Amboim.

Description

The shell is compressed, moderately involute, with about 60 per cent of the preceding whorl covered by the outer whorl. The umbilicus is moderately narrow (22% of the diameter), with steep umbilical walls and evenly rounded umbilical shoulders. The whorl section is oval, compressed ($w/h = 0,83$) with an evenly rounded venter. There are an estimated five constrictions per half-whorl, preceded by a strong ventral rib. Flank and venter also bear faint, ill-preserved, fine ribs.

Measurements

No.	D	H	W	w/h	U
SAM–6407	37	18(49)	15(41)	0,83	$\pm 8(22)$

Discussion

The specimen cannot be usefully compared with the large number of late Albian puzosiids known, although if the estimated number of constrictions is correct, it must approach forms such as *P. crebrisulcata* Kossmat (1898: 116, pl. 17 (fig. 4), pl. 18 (fig. 2) and *P. malandiandrensis* Collignon (1963: 66, pl. 265 (fig. 1156)).

Puzosia (Puzosia) cf. sharpei Spath, 1923

Fig. 35

Compare

Ammonites planulatus Sharpe (*non* Sowerby), 1854: 29, pl. 12 (fig. 4 only).

Puzosia sharpei Spath, 1923: 46, pl. 1 (figs 11–12), fig. 11b. Renz, 1968: 21, pl. 1 (figs 4, 8), figs 6b, 7e (with synonymy).

Material

A single fragment, SAM–PCA3141, preserved as an internal mould, from the *dispar* Zone of Praia-Egito.

Description

The single specimen is a fragment of about one-quarter whorl. The shell was moderately evolute, with a fairly wide, shallow umbilicus and evenly rounded umbilical shoulders. The flanks are broad, subparallel and only slightly convex, with a broadly rounded venter. There are two deep constrictions on the fragment, separated along the venter by a distance slightly greater than the whorl height. The constrictions are initially prorsiradiate, but soon recurve before flexing strongly forwards to form a chevron across the venter.

Discussion

The Angolan material differs from *P. sharpei* in that the constrictions do not show as strong a geniculation, and are therefore not as strongly falcate.

Wiedmann & Dieni (1968) included this species in the synonymy of *Puzosia provincialis* (Parona & Bonarelli), a lower Middle Albian species. The material figured by these authors (1968) as *P. provincialis* shows relict lappet structures and are, therefore, microconchs. The holotype of *P. sharpei*, on the other hand, is still septate at 83 mm diameter and appears to be a macroconch. Consequently, the authors regard the inclusion of *P. sharpei* into the synonymy of *P. provincialis* as premature, and prefer to maintain Spath's species as distinct, for the time being.

Occurrence

Puzosia sharpei is known with certainty only from southern England, France, Switzerland, and possibly Angola, where it is typical of the *dispar* Zone.



Fig. 35. *Puzosia (Puzosia) cf. sharpei* Spath. Lateral and ventral views of SAM-PCA3141. $\times 1$.

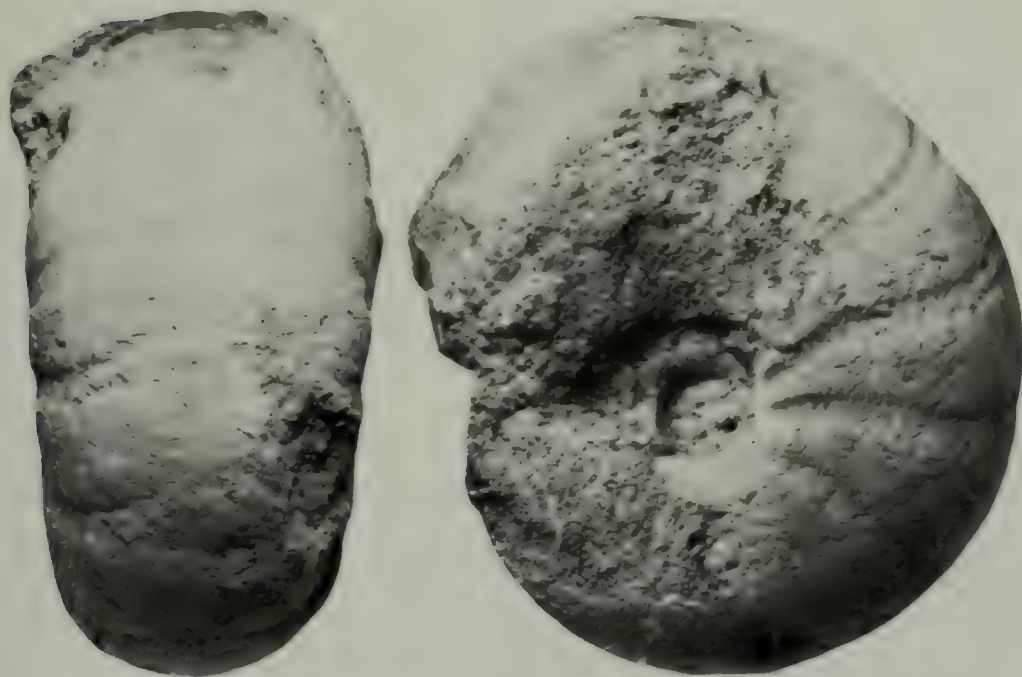


Fig. 36. *Desmoceras (Desmoceras) latidorsatum* (D'Orbigny). The original of D'Orbigny's (1841, pl. 80 (fig. 5)) figured specimen from the Middle Albian of France, in the D'Orbigny collection, Natural History Museum, Paris. $\times 1$.

Subfamily Desmoceratinae Zittel, 1895

Genus *Desmoceras* Zittel, 1884

Subgenus *Desmoceras* Zittel, 1884

Type species *Ammonites latidorsatus* Michelin, 1838

Desmoceras (Desmoceras) latidorsatum perinflatum subsp. nov.

Figs 37–38, 39D–F

Desmoceras latidorsatum var. *inflata* Breistroffer, Haas, 1952: 2, figs 1, 3–10.

Desmoceras reynesianum Haas, 1952: 4, figs 2, 11–13.

Material

Twenty-one specimens, SAM-6414, SAM-PCA2931, 2934, 2968, 3170 and 3172 from Egito, preserved as composite internal moulds, and USNMNH 236961–75 from Porto Amboim with recrystallized shell generally preserved.

Type material

USNMNH 236970 from Porto Amboim is designated holotype; the remaining specimens are paratypes.

Etymology

From the Latin, *per*—exceedingly, very much, *inflatus*—swollen; applying to the strongly inflated shell form.

Diagnosis

A rather small, late Albian (*dispar* Zone) subspecies of *D. latidorsatum* in which the majority of the population comprises strongly inflated individuals ($W/H = 1.10-1.50$) which correspond to the *D. latidorsatum* var. *inflatum* of previous workers.

Description

Very involute, cadicone, with a narrow, crater-like umbilicus (16–20% of diameter). Umbilical walls steep, with gently rounded shoulders. Flanks flattened (USNMNH 236972) to strongly convex (USNMNH 236964), with maximum width just below mid-flank. Venter broadly rounded. Shell smooth,



Fig. 37. *Desmoceras* (*Desmoceras*) *latidorsatum perinflatum* subsp. nov. A–B. USNMNH 236966. C–E. The holotype USNMNH 236970. F–G. USNMNH 236973. H–J. USNMNH 236768. K–L. USNMNH 236967. M–O. USNMNH 236964. $\times 1$.

except for weak constrictions on some specimens (USNMNH 236970). Where present, constrictions begin at the umbilical seam and pass strongly forwards to the umbilical shoulder where they recurve strongly, flexing forwards again just above mid-flank to form a prominent U-shaped tongue across the venter.

Measurements

No.	D	H	W	W/H	U
USNMNH 236961	21	±9(43)	±12(57)	1,33	±4(19)
USNMNH 236962	14	7(50)	8,5(61)	1,21	2,3(16)
USNMNH 236964	27	13(48)	18,3(68)	1,41	±5(18)
USNMNH 236965	21	11,5(55)	14(67)	1,22	?
USNMNH 236966	23	9,5(41)	13(56)	1,37	±4,5(20)
USNMNH 236967	20	10,2(51)	12(60)	1,18	±4(20)
USNMNH 236968	12,3	6,2(50)	8,3(67)	1,34	±2(16)
USNMNH 236969	42	22(52)	±24(57)	1,09	±8(9)
USNMNH 236970	24	11(46)	15(63)	1,36	4,5(19)
USNMNH 236971	14,6	7,5(51)	9(62)	1,20	?
USNMNH 236972	15	6(40)	8,5(57)	1,42	2,7(18)
„	10,5	5(48)	6,5(62)	1,30	2,0(19)
USNMNH 236973	13	±6(46)	8,1(62)	1,35	?
USNMNH 236975	±14	6,5(46)	8,2(59)	1,26	2,2(16)

Intraspecific variation

The wide range of intraspecific variation shown by *D. (Desmoceras) latidorsatum* has long been recognized (D'Orbigny 1941, Pictet (*in* Pictet & Roux) 1848, Kossmat 1897, Jacob 1908, Fallot 1910, Spath 1923, Wiedmann & Dieni 1968) and it would appear that species separation is possible only at the population level since gross intraspecific variation exceeds subtle differences between successive faunas. Consequently, the following names, which are used both at the varietal and subspecific levels by various authors, are based merely upon individuals within these populations and are of no taxonomic value: *media* (Jacob), *complanata* (Jacob), *inflata* (Breistroffer), *obesa* (Reynès), *petkovici* Breistroffer, *longesulcata* (Collignon) and *angusteumbilicata* Haas.

Jacob (1908) studied the intraspecific variation within *Desmoceras latidorsatum* from the Balme de Rencurel, a fauna contemporaneous with D'Orbigny's (1841) material (Fig. 36) from the 'Argile à *Hoplites dentatus* Sow.' of Aube, and of early Middle Albian age. Within this assemblage, Jacob (1908) recognized the typical form, as well as his varieties *media* and *complanata* which are more compressed than typical *D. latidorsatum*. In contrast, the present collection, together with that described by Haas (1952) shows that inflated variants, normally assigned to the variety *inflata* Breistroffer, form the vast majority of the populations from the *S. dispar* Zone of Angola (Fig. 38), whereas compressed

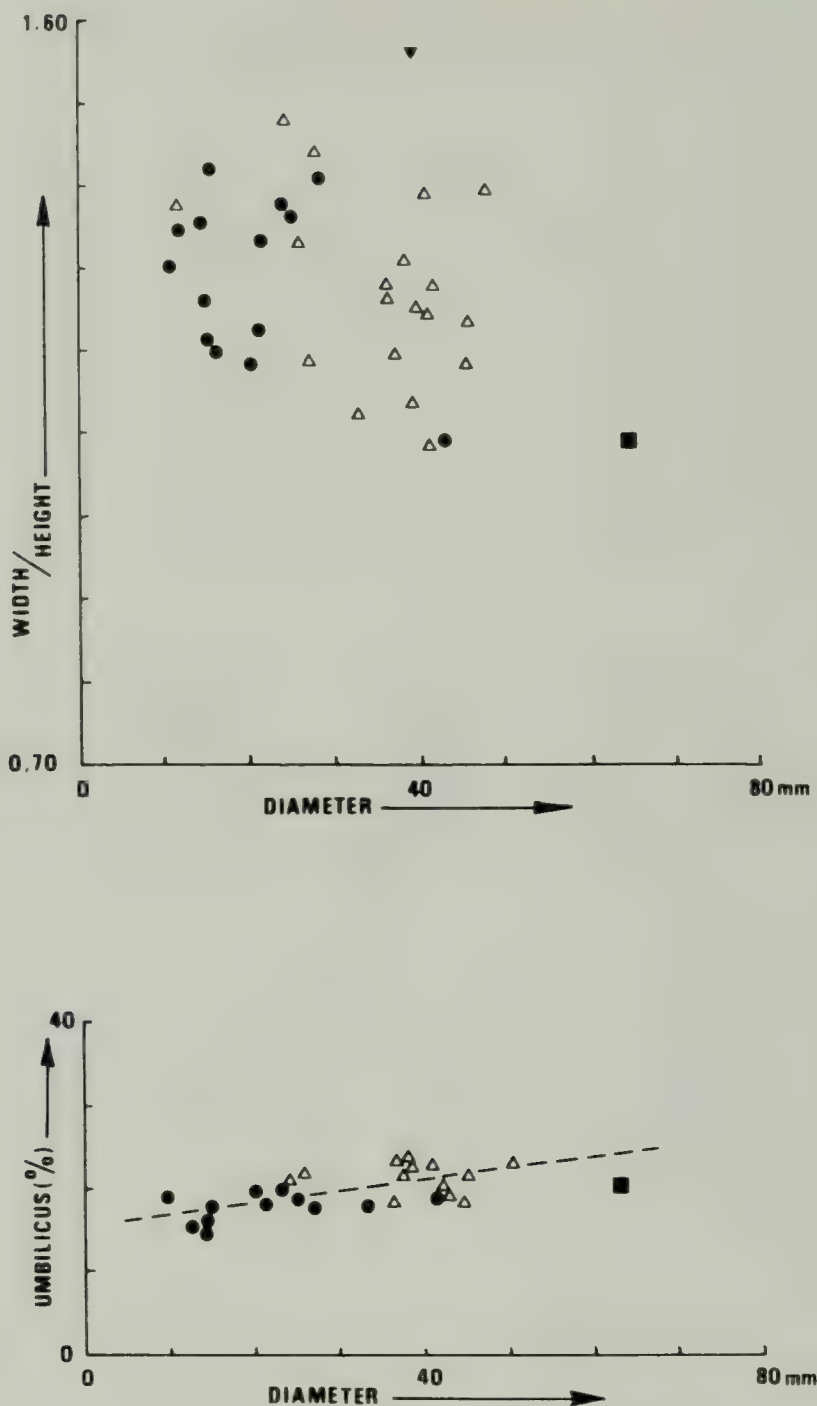


Fig. 38. Plot of inflation and umbilical ratio against diameter for *Desmoceras latidorsatum perinflatum* subsp. nov. Dots = present Angolan material; open triangles = material described by Haas (1952), and Wiedmann & Dieni (1968); black triangle = *Desmoceras reynesianum* (after Haas 1952); square = *Desmoceras latidorsatum latidorsatum* (Michelin), (after D'Orbigny 1841).

forms are entirely absent. It would seem, therefore, that there has been a genuine shift within the population structure of *D. latidorsatum* through time, from predominantly compressed individuals in the Middle Albian to predominantly inflated variants in the uppermost Albian. The observation that certain individuals throughout this range can be assigned to *Desmoceras latidorsatum* s.s. suggests that the differences are not of specific importance. Since the Angolan population comprises mainly strongly inflated individuals ($W/H = 1.10-1.50$), the differences are sufficient for subspecific separation and the entire Angolan population (it is the characters of the population which define the subspecies) is assigned to *D. latidorsatum perinflatum* subsp. nov.

Desmoceras reynesianum Haas (1952: 4, figs 2, 11-13) was proposed to replace *Ammonites obesus* Reynès (non Stoliczka) and is characterized by its extreme inflation. The Angolan material assigned to this species, however, differs in being of uppermost Albian age and, as can be seen from Figure 38, merely represents extreme variants within the present population, and consequently Haas's (1952) material is included in the synonymy of *D. latidorsatum perinflatum* subsp. nov.

Discussion

Population studies will probably show that *D. collignoni* Breistroffer (in Besairie 1936: 170, pl. 16 (fig. 2), fig. 10d), *D. inane* (Stoliczka) (1865: 121, pl. 59 (figs 13-14)) and *D. chirichense* (Pervinquière) (1907: 152, pl. 6 (figs 17-20)) do not bear separation from *D. latidorsatum*. *Desmoceras barryae* Anderson (1958: 214, pl. 12 (fig. 2)) and *D. merriami* Anderson (1902: 103, pl. 6 (figs 135-138)), which was treated as a variety of *D. latidorsatum* by Breistroffer (1947: 61), are probably better referred to the subgenus *Pseudouhligella*.

Occurrence

Desmoceras latidorsatum perinflatum subsp. nov. is currently known with certainty only from Angola.

Superfamily ACANTHOCERATACEAE Hyatt, 1900

Family Lyelliceratidae Spath, 1921

Discussion

Wright (in Arkell *et al.* 1957) included the following genera within the Lyelliceratidae—*Prolyelliceras*, *Lyelliceras*, *Tegoceras*, *Neophlycticeras*, *Stoliczkaia* (with *Faraudiella* as a subgenus), *Budaiceras* and *Salaziceras*. More recently, Casey (1965) introduced the subgenus *Stoliczkaia* (*Villoutreysia*), and proposed the new genus *Paradolphia* for forms from the *S. dispar* Zone of southern England said to be transitional between *Stoliczkaia* and *Forbesiceras*. Matsumoto & Inoma (1975: 277) have also introduced the subgenus *Stoliczkaia* (*Shumarinaia*).

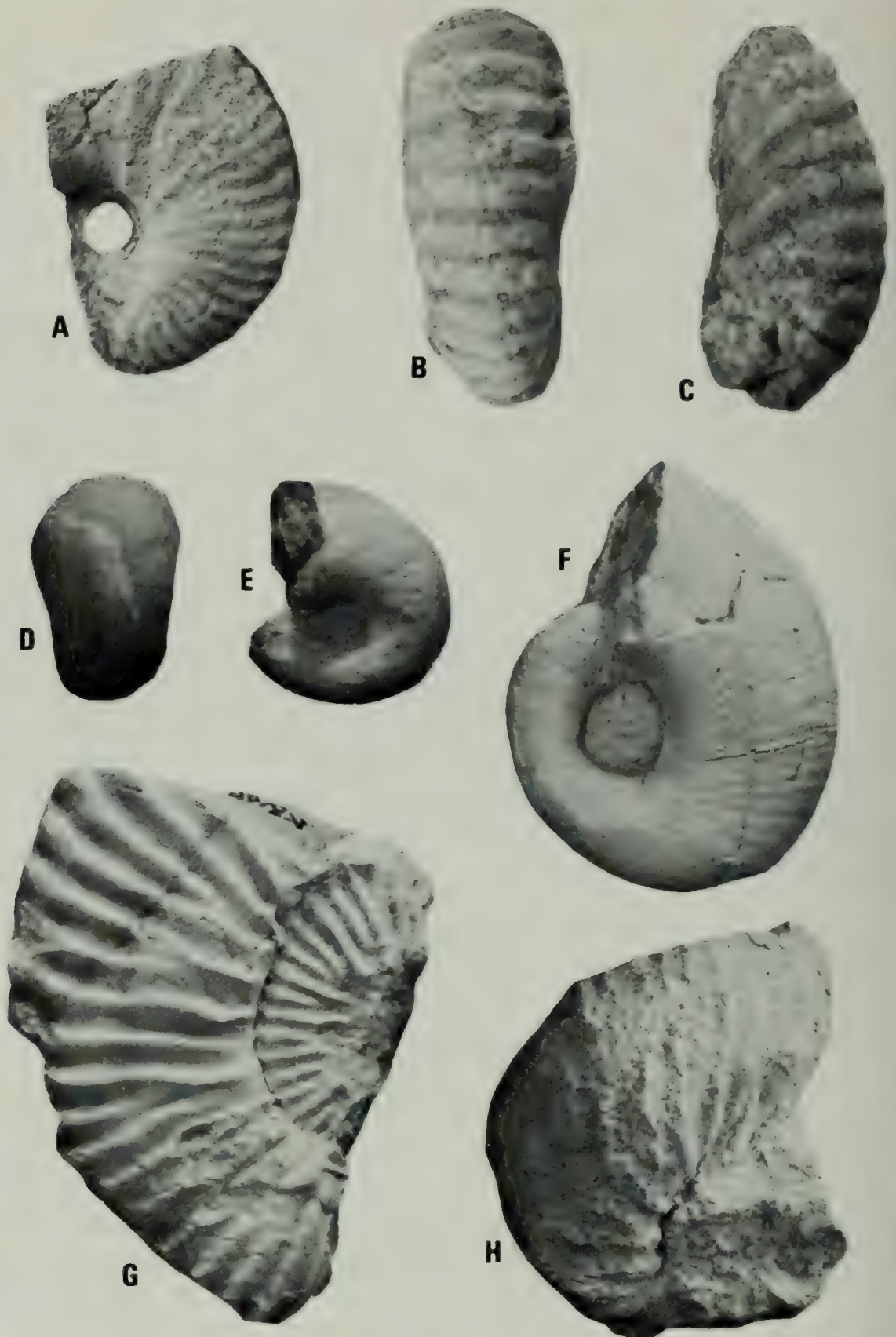


Fig. 39. A. *Stoliczkaia* (*Stoliczkaia*) *tenuis* Renz. Lateral view of SAM-PCA5478. B-C. *Stoliczkaia* (*Stoliczkaia*) sp. A fragmentary internal mould, SAM-PCA4805, from Cabo Ledo. D-F. *Desmoceras latidorsatum perinflatum* subsp. nov. D-E. Ventral and lateral views of SAM-PCA2934. F. Lateral view of SAM-PCA2931. G. *Mortonicerias* (*Angolaites*) *gregoryi* (Spath). Lateral view of a crushed fragment, SAM-PCA3168. H. *Mariella* aff. *circumtaeniatus* (Kossmat). SAM-PCA3130, from low in the sea cliffs (lower part of *dispar* Zone) at Praia-Egito. $\times 1$.

Amedro (1976) has recently suggested that *Paradolphia* is better regarded as a subgenus of *Neophylticeras* (along with *Protissotia* and *Eotropitoides*), whilst there is a case for regarding both *Paracalycoceras* and *Cottreautes*, both of which derive from *Stoliczkaia*, as Lyelliceratidae rather than Acanthoceratidae.

The collection of *Stoliczkaia* to be discussed below shows a remarkable similarity to the earliest *Forbesiceras*, i.e. the *beaumontianum*–*largilliertianum* group (compare Juignet & Kennedy 1977, pl. 6 (fig. 1)), and both from a stratigraphic and morphological point of view is most likely to have provided the ancestor to *Forbesiceras*. The close similarity between *Forbesiceras* and *Stoliczkaia* of the *dispar*–*clavigera* group suggests that the monogeneric subfamily Forbesiceratinae is superfluous, and that *Forbesiceras* should be transferred to the Lyelliceratidae. A study of the early ontogenetic stages of *Forbesiceras* has led Casey (1965) to suggest that *Neopulchellia* (Collignon 1929) was based upon pyritic nuclei of *Forbesiceras*.

Genus *Stoliczkaia* Neumayr, 1875

Type species *Ammonites dispar* d'Orbigny, 1841

Discussion

Stoliczkaia occupies a key position in the evolution of the mid-Cretaceous Acanthocerataceae, as it appears to be the origin of both the Mantelliceratinae and Acanthoceratinae which in turn gave rise to the remaining Upper Cretaceous acanthoceratids.

More than a score of specific names have been applied to the genus, but there has been no sound account of intraspecific variation, nor of the apparent dimorphism present, some subgenera and species reaching a large size and becoming feebly ribbed at maturity (e.g. *S. (S.) dispar*), others remaining small with strong ribs throughout (*S. (Shumarinaia)*). Furthermore, because of their transitional position between Lyelliceratidae, Acanthoceratinae and Mantelliceratinae, there are a number of forms whose position is equivocal. Indeed, the authors find themselves in disagreement over the precise position of some of these passage forms.

The subgenera of *Stoliczkaia* are as follows:

1. *Stoliczkaia (Stoliczkaia)* (type species *Ammonites dispar* d'Orbigny). Typically rather involute, compressed ammonites with straight or slightly curved primary ribs, with shorter intercalated ribs between. Primary ribs may be weakly bullate, and during early growth stages bear ventrolateral tubercles or clavi, whilst the venter may be flat or slightly raised. In middle growth tuberculation disappears and ribs extend across a rounded venter; at maturity ribs broaden, become irregular, and may become effaced on the adult body chamber. Typical representatives of the type species *S. (S.) dispar* are shown as Figures 40 and 41.
2. *Stoliczkaia (Faraudiella)* (type species *Ammonites blancheti* Pictet & Campiche). Small *Stoliczkaia* in which distinct siphonal, and sometimes ventro-

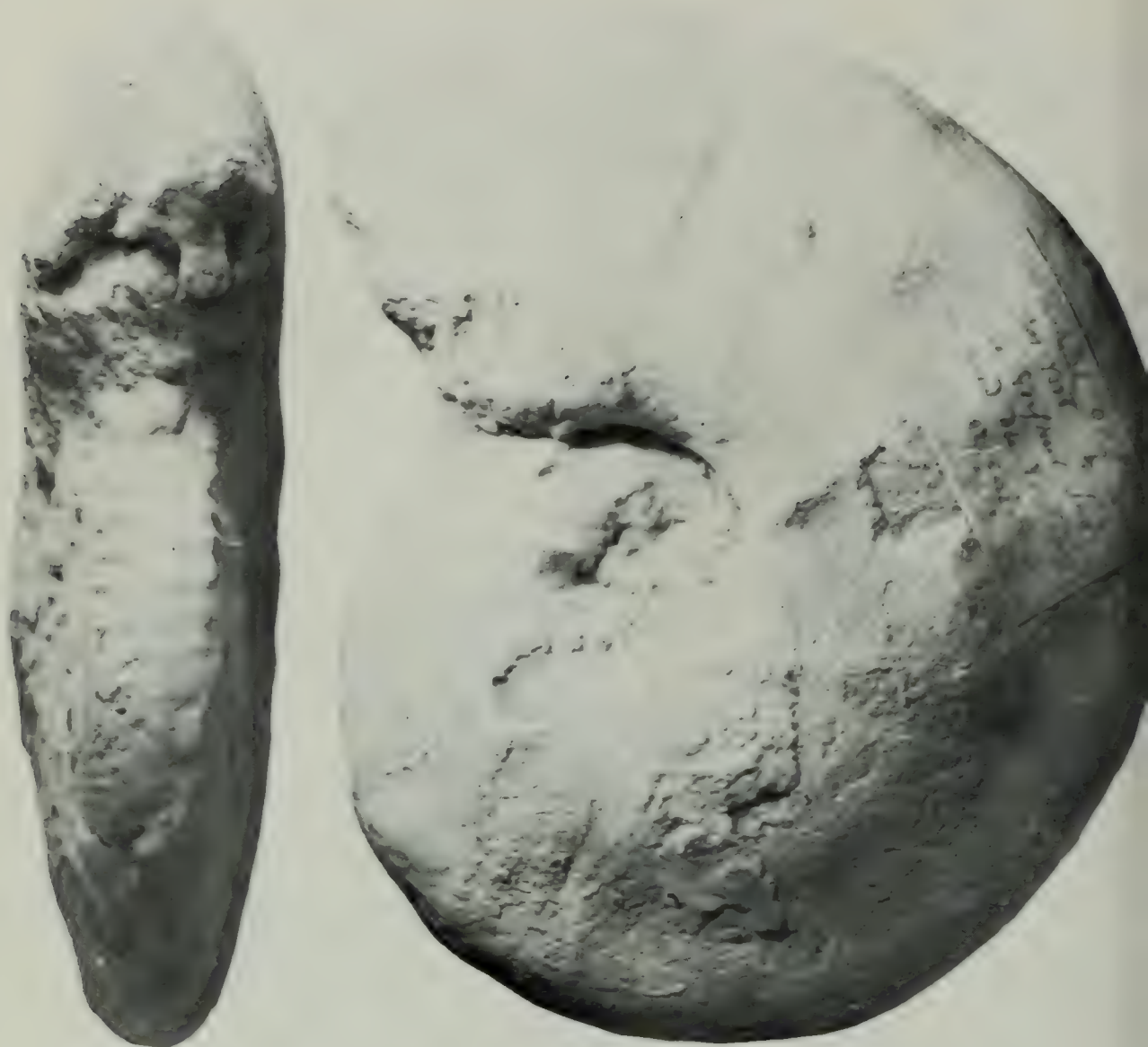


Fig. 40. *Stoliczkaia* (*Stoliczkaia*) *dispar* (d'Orbigny). The holotype, Renaux collection, Faculté des Sciences, Montpellier, from the Upper Albian of Ventoux, Vaucluse, France. Slightly reduced.

lateral tubercles persist on to the body chamber. Typical representatives are shown in Figure 42.

3. *Stoliczkaia* (*Shumarinaia*) (type species *S.* (*Shumarinaia*) *hashimotoi* Matsumoto & Inoma). Small, with simple suture line and coarse ribbing throughout.

A fourth subgenus, *Villoutreysia* was proposed by Casey (1965: 435, fig. 161; type species *S.* (*V.*) *villoutreysi* Casey) (Fig. 43) for what he described as *Hypacanthoplites* homoeomorphs diagnosed as '*Stoliczkaia* with broad, square venter and strong persistent ribbing, differing from *Mantelliceras* in much

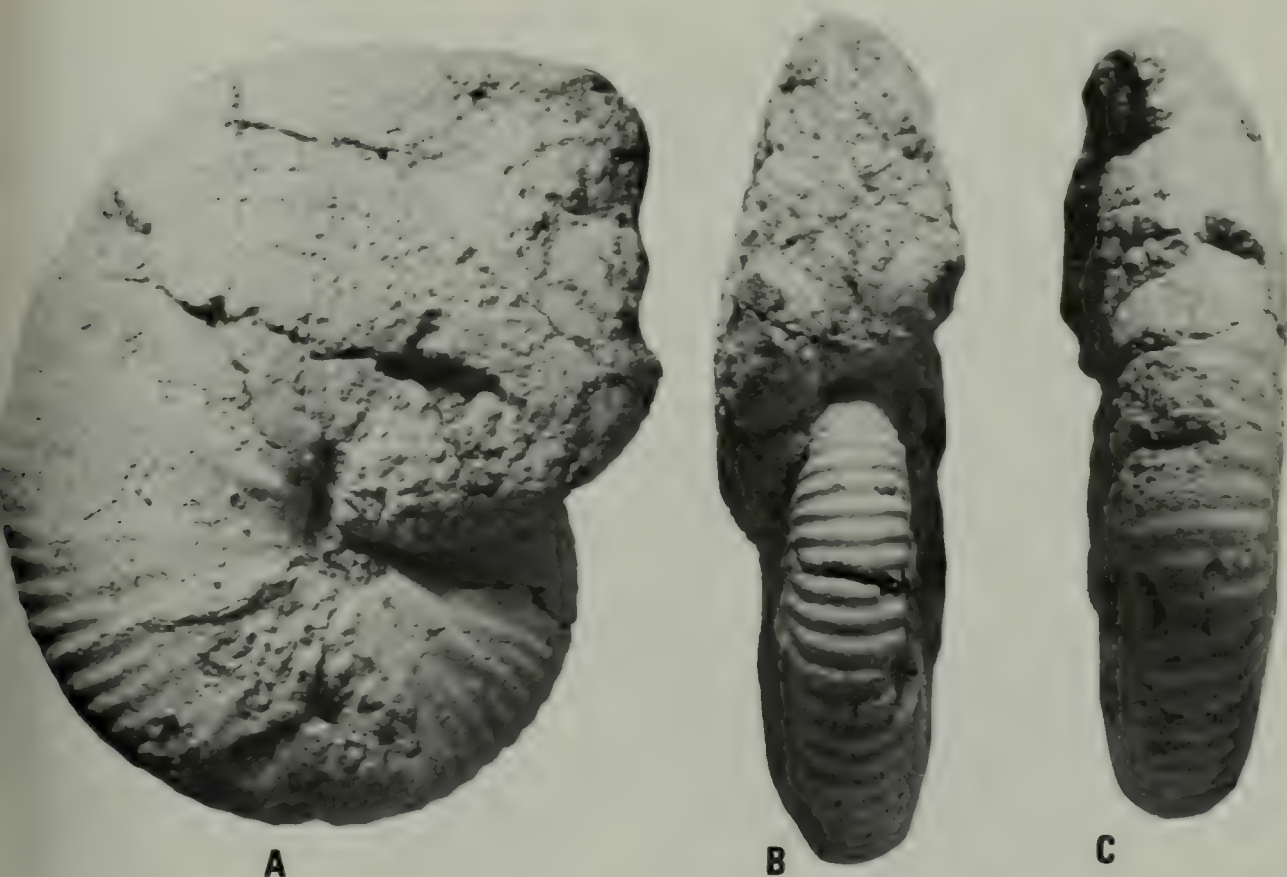


Fig. 41. *Stoliczkaia* (*Stoliczkaia*) *dispar* (d'Orbigny). Juvenile specimen in C. W. Wright collection WW 72344, from the *dispar* Zone Ammonite Bed of the Dorset Coast. $\times 1$.



Fig. 42. *Stoliczkaia* (*Faraudiella*) *sexangulata* (Seeley). Seeley's original specimen, Sedgwick Museum, Cambridge, B53, from the Cambridge Greensand, Cambridge. $\times 1$.

earlier loss of ventral tubercles, squarer whorls and, generally, narrow and shallower umbilicus'. The holotype of *S. (V.) villoutreysi* is illustrated here as Figure 43; after an examination of the large collections of *Stoliczkaia* in the Paris Museums the authors have concluded that it is not separable subgenerically from *Stoliczkaia sensu stricto*.

The genus *Paradolphia* Casey was proposed (Casey 1965: 461, pl. 77 (figs 5–6)) for the type species *P. prisca* Casey (illustrated here as Fig. 44) for intermediates between *Stoliczkaia* and *Forbesiceras* but, as noted above, is possibly a subgenus of *Neophlycticeras*.

Paracalycoceras (type species *Ammonites wiestii* Sharpe 1857: 47, pl. 21 (fig. 3)) is an enigmatic genus from the Lower Cenomanian of southern England, known with certainty only from two specimens—the lost holotype (*fide* Kennedy 1971) and an extant specimen in the collections of C. W. and E. V. Wright (Fig. 45). Kennedy (1971: 79) diagnosed the genus as follows: 'Medium-sized, somewhat involute ammonites. Inner whorls slightly compressed, with long ribs bearing umbilical bullae, and lower and upper ventrolateral tubercles separated by 1, 2, or sometimes more shorter ribs. There is a distinctly raised siphonal area, and an incipient siphonal tubercle on all ribs. Outer whorl with a broad venter, and broad, distant, flexuous rursiradiate ribs, irregularly long and short.'

Both morphologically and in the observed ontogenetic changes, *Paracaly-*

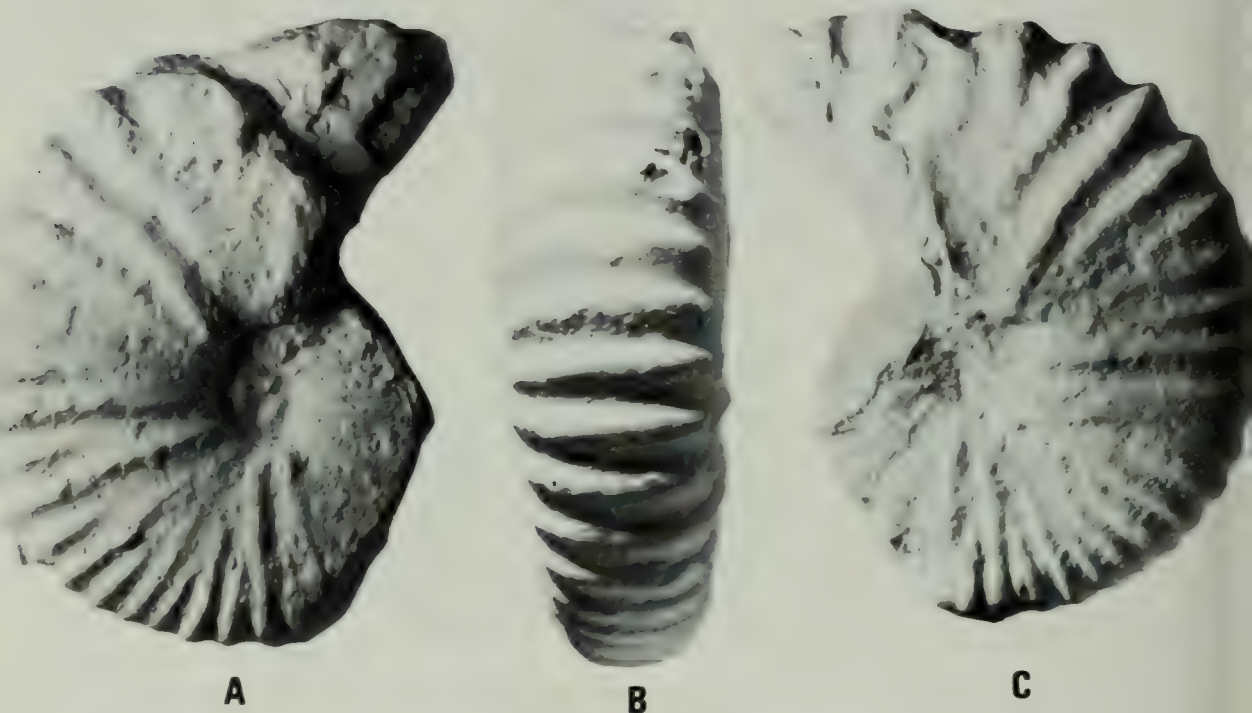


Fig. 43. *Stoliczkaia (Stoliczkaia) villoutreysi* Casey. Holotype, O. de Villoutreys collection, Uppermost Albian, Monte Carlo Tunnel, Monte Carlo. $\times 1$.

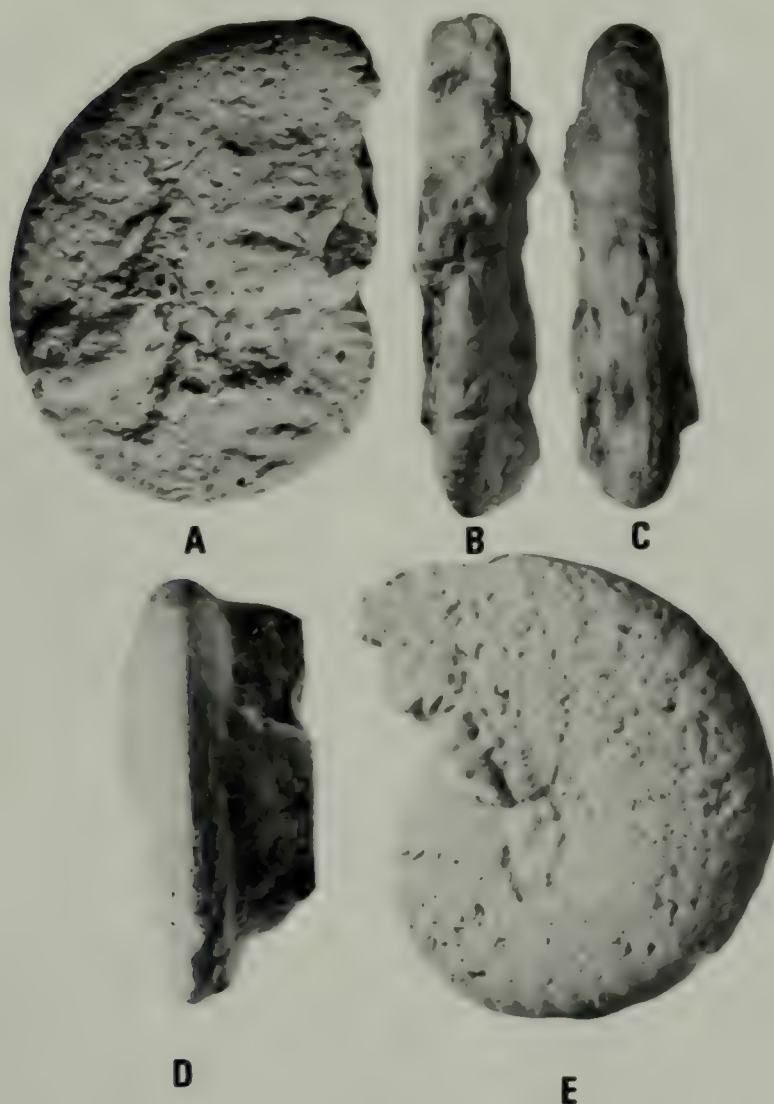


Fig. 44. *Neophylticeras* (*Paradolphia*) *prisca* (Casey). A-C. Holotype, Norwich Castle Museum 61.18(1679). D-E. Paratype, Sedgwick Museum, Cambridge, B93303. Both from the Cambridge Greensand, Cambridge. A-C $\times 1$, D-E $\times 2$.

coceras is virtually indistinguishable from certain species of *Stoliczkaia*, from which it is obviously descended. Little more can be said until toptype material is studied, but it may prove more satisfactory to regard it as a subgenus of *Stoliczkaia*.

Kennedy (1971: 80) considered that the genus *Cottreautes* (Collignon 1929), based upon pyritic nuclei, 'may be wholly or partly a synonym of *Paracalycoceras*'. Again, this question cannot be resolved until *Paracalycoceras* is better known or mature *Cottreautes* are described. It seems very likely, however, that some *Cottreautes* are juveniles of either *Stoliczkaia* or *Paracalycoceras*, and that it should be considered a *nomen dubium*.



Fig. 45. *Stoliczkaia* (*Paracalycoceras*) *wiestii* (Sharpe). C. W. Wright collection 3556, Lower Cenomanian, Cenomanian Limestone, Bed A2, White Cliff, Seaton, Devon. $\times 1$.

Subgenus *Stoliczkaia* (*Stoliczkaia*) Neumayr, 1875

Renz (1968: 46) recognized four species groups within *Stoliczkaia sensu stricto*:

1. The group of *S. dispar* with ventrolateral tubercles only on the inner whorls and weak ribbing on the body chamber, comprising *S. dispar* (d'Orbigny), *S. dorsetensis* Spath and *S. tenuis* Renz.
2. The group of *S. africana* which retains ventrolateral tubercles on to the body chamber, with well-developed, broad, falcate ribs, and includes *S. africana* (Pervinquière) and *S. flexicostata* Breistroffer. Matsumoto & Inoma (1975) have proposed the subgenus *Shumarinaia* for this group.
3. The group of *S. notha*, which lacks ventrolateral tubercles whilst retaining strong ribbing on to the body chamber, and comprises *S. notha* (Seeley) and *S. clavigera* Neumayr.
4. The group of *S. levis* which lacks ventrolateral tubercles and is virtually without ornament. Only *S. levis* Renz, based on a unique holotype, is assigned to this group.

Stoliczkaia (*Stoliczkaia*) *tenuis* Renz, 1968

Figs 46–53, 54A–F, 55, 68E

Stoliczkaia tenuis Renz 1968: 48, pl. 6 (figs 6, 12), fig. 16b, f.

Material

37 specimens, USNMNH 236981–237012a–b, 237014–5, together with 3 specimens in the collections of the South African Museum, SAM-PCA5477–78 and 6811, all retaining part or all of their recrystallized shell, from Porto Amboim, and 7 specimens, SAM-PCA2938–39, 2944, 3169, 3373 and 5475–5476, preserved as composite internal moulds from Egito.

Description

Up to 20 mm diameter: shell compressed ($W/H = 0.50–0.63$), very involute with a deep, narrow umbilicus (11–17% of diameter). Umbilical walls steep, almost vertical, with evenly rounded umbilical shoulders. Flanks broad, slightly convex to flat, with maximum width below mid-flank, converging towards the narrow venter. Venter slightly convex to almost tabulate, and weakly raised along the siphonal line. Ornament comprises thirteen to sixteen prorsiradiate ribs per half-whorl, generally alternating long and short. The ribs are more or less strongly flexed and bear distinct ventrolateral tubercles. The latter are joined across the venter by convex ribs.

Up to a diameter of 12 mm in USNMNH 237005 (10 mm in USNMNH 237012) ribs appear to be absent, although there are weak tubercles possibly marking their position along the ventrolateral shoulders. In USNMNH 237010, the main ribs are ornamented by rather distinct umbilical bullae.

21–40 mm diameter: shell compressed ($w/h = 0,53-0,68$), very involute (umbilicus 15–17% of diameter), with a high rectangular whorl section. Ribbing denser (twenty to twenty-four ribs per half-whorl), not infrequently with two intercalatories between main ribs. The ventrolateral tubercles are generally still prominent at this stage.

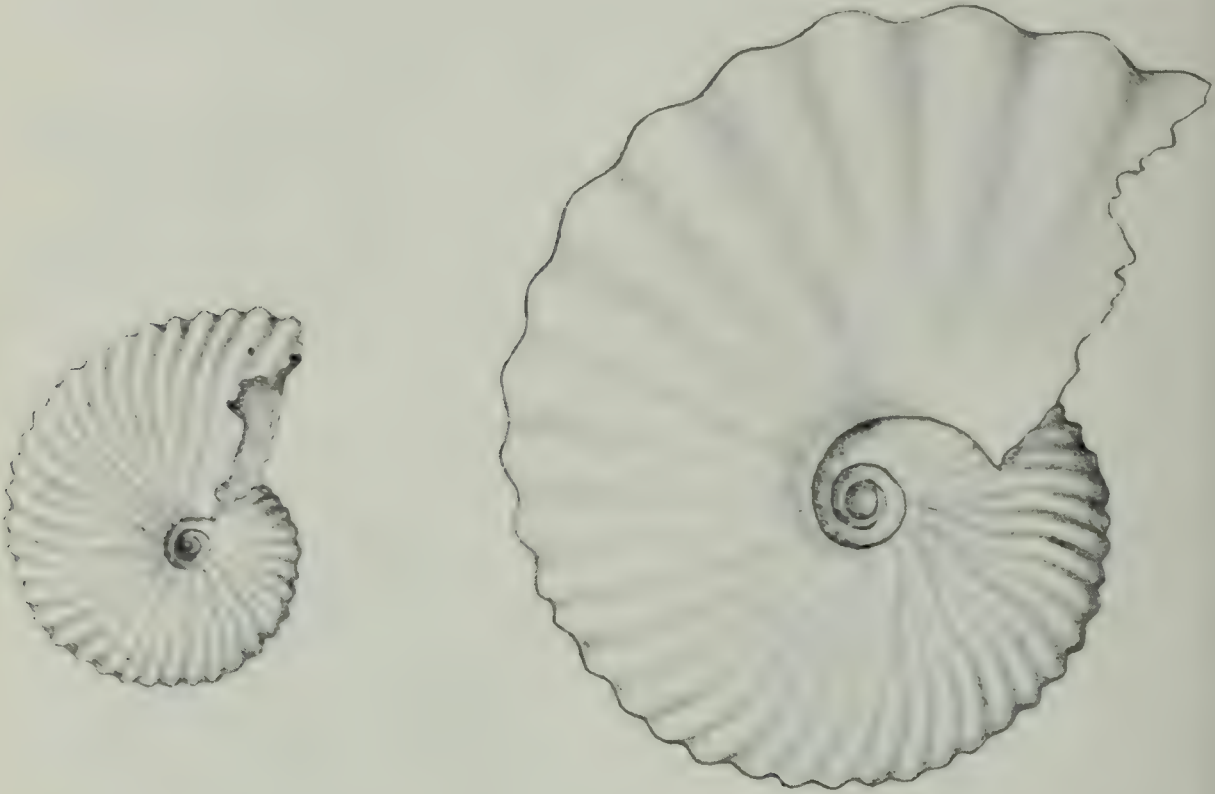


Fig. 46. *Stoliczkaia* (*Stoliczkaia*) *tenuis* Renz. Reconstructed juvenile and middle growth stages. $\times 1$.

41–70 mm diameter: the ventrolateral tubercles are commonly lost between 40–45 mm diameter (37 mm in USNMNH 236996) and the ribs pass uninterrupted across the venter, sometimes with a slight thickening in the ventrolateral position. The shell becomes slightly more inflated ($w/h = 0,58-0,69$), with distinctly convex flanks and a rounded venter. The flank ribs coarsen considerably and there are commonly one or two intercalatories between long ribs, although in USNMNH 236994 and USNMNH 236987 there are probably more long ribs than intercalatories. Where there are two intercalatories between long ribs they may be of markedly different lengths (USNMNH 236984). Immediately prior to the aperture, all ornament is lost and the body chamber becomes smooth (USNMNH 236981).



Fig. 47. *Stoliczkaia (Stoliczkaia) tenuis* Renz. A-C. USNMNH 236999. D-F. USNMNH 237009. G-I. USNMNH 237006. J-L. USNMNH 237010. M-O. USNMNH 237015. P-R. USNMNH 237014. S-U. 236997. V-X. USNMNH 237003. $\times 1$.



Fig. 48. *Stoliczkaia* (*Stoliczkaia*) *tenuis* Renz. A-C. USNMNH 236988. D-F. USNMNH 237003. G-I. USNMNH 236990. $\times 1$.

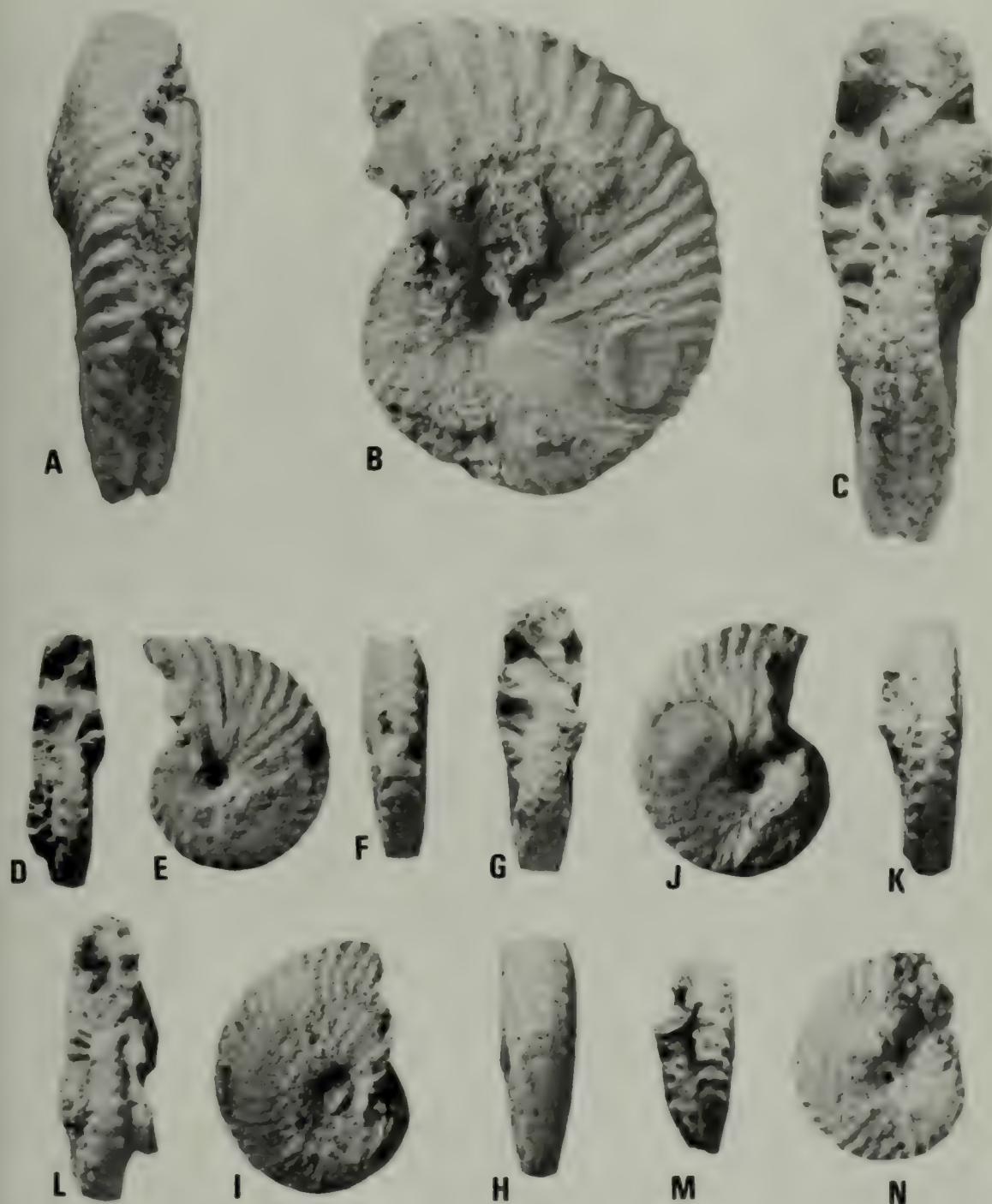


Fig. 49. *Stoliczkaia (Stoliczkaia) tenuis* Renz. A-C. USNMNH 236945. D-F. USNMNH 237004. G-I. USNMNH 237000. J-L. USNMNH 237001. M-N. USNMNH 237007. $\times 1$.



Fig. 50. *Stoliczkaia (Stoliczkaia) tenuis* Renz. A-C. USNMNH 236985. D-F. USNMNH 236984. $\times 1$.

Measurements

No.	D	H	W	w/H	U
USNMNH 236983	66	32(48)	$\pm 22(33)$	0,69	10(15)
USNMNH 236985	65	36(55)	26(40)	0,72	$\pm 13(20)$
USNMNH 236986	± 56	29(52)	17,6(31)	0,61	$\pm 9(16)$
USNMNH 236987	67	35(52)	$\pm 23,5(35)$	0,67	$\pm 9,7(14)$
USNMNH 236988	68	33(48)	?	?	11,1(16)
„	50	26(52)	18(36)	0,69	$\pm 9(18)$
USNMNH 236989	55,5	27,5(50)	$\pm 19(34)$	0,69	$\pm 10(18)$
USNMNH 236990	26	13,5(52)	7,2(28)	0,53	?
USNMNH 236992	38	$\pm 19(50)$	$\pm 10(26)$	0,53	?
USNMNH 236994	50	26(52)	15,2(30)	0,58	7,7(15)
USNMNH 236995	55	30(54)	18,7(34)	0,62	7,9(14)
USNMNH 236996	37	17,5(47)	$\pm 12(32)$	0,68	?
USNMNH 236997	35	18(54)	9(26)	0,50	6(17)
USNMNH 236998	34	19(56)	$\pm 10(29)$	0,52	5,5(16)
USNMNH 236999	34	19(56)	11(32)	0,58	5(15)
„	26	14(54)	7,5(29)	0,54	?
USNMNH 237000	30	15(50)	9(30)	0,60	?
USNMNH 237001	30	15,7(52)	8,3(28)	0,53	4,7(16)
„	20,5	10,8(53)	5,5(27)	0,51	2,5(12)
USNMNH 237002	30	$\pm 16,5(55)$	8,5(28)	0,51	?
USNMNH 237003	31,3	17(54)	10(32)	0,59	$\pm 4,5(14)$
USNMNH 237004	28	15(54)	8(29)	0,53	4(14)
„	17,5	9,5(54)	6(34)	0,63	2,7(15)
USNMNH 237005	17,3	9(52)	$\pm 4,5(26)$	0,50	$\pm 3(17)$
USNMNH 237006	17,7	9(51)	5(28)	0,56	2(11)
„	12,3	6(49)	3,4(28)	0,57	?
USNMNH 237008	21	11(52)	6(29)	0,54	3(14)
„	15	7(47)	4(27)	0,57	2,2(15)
USNMNH 237010	17	8(47)	4,5(26)	0,56	2,5(15)
USNMNH 237012	9,5	4(42)	3(32)	0,75	$\pm 1,5(16)$

Intraspecific variation

The large number of well-preserved specimens available to the authors permits a better understanding of the intraspecific and ontogenetic variation in this species. The marked ontogenetic change in ornament shown by this species has been outlined above. However, Figure 55 also shows that there is considerable variation in the degree of inflation of the whorls ($w/H = 0,50-0,72$), with a distinct tendency for the whorls to become more inflated at large diameters. Furthermore, Figure 55 shows that not only is there some variation in the width of the umbilicus, but there is also a slight tendency for the shell to become more evolute with growth.



Fig. 51. *Stoliczkaia (Stoliczkaia) tenuis* Renz. A-D. USNMNH 236994. $\times 1$.

Discussion

As shown above, the present material is rather variable, and the type of *S. (S.) tenuis* and the specimen referred to as *S. (S.)* aff. *tenuis* by Renz (1968, pl. 6 (fig. 12)) fall within this range.

When mature, *S. tenuis* closely resembles *S. (S.) clavigera* Neumayr (= *Ammonites dispar* Stoliczka (*non* d'Orbigny) 1865: 45, pl. 85 (figs 1–3 only)) (see Fig. 56), from which it appears to differ only in being consistently more compressed. Further work may show that the two merit only subspecific separation.

S. (Stoliczkaia) dispar (d'Orbigny) (1841: 143, pl. 45 (figs 1–2)) is a widely-cited but much misinterpreted species. Consequently, the holotype is here photographically figured for the first time (Fig. 40), as well as a typical specimen from the *dispar* Zone of Dorsetshire, England (Fig. 41). *S. (Stoliczkaia) dispar* differs from the present species in having far more (up to nine) intercalatories between long ribs, whilst the latter are ornamented with weak umbilical bullae. The venter loses its ventrolateral tubercles and becomes rounded at smaller diameters and the body chamber ornament is also different; in *S. (S.) dispar*, ribbing rapidly weakens in maturity (at least on the internal mould) and all that

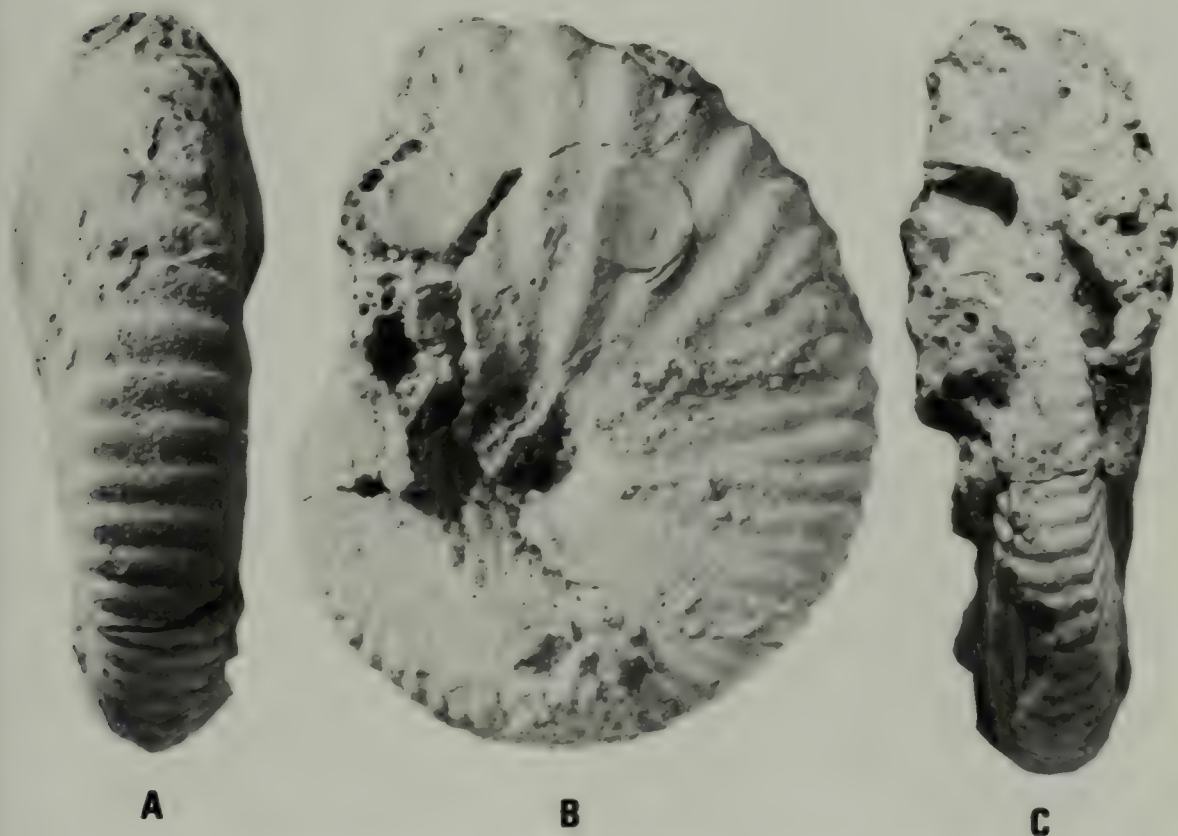


Fig. 52. *Stoliczkaia (Stoliczkaia) tenuis* Renz. A–C. USNMNH 236987. $\times 1$.



Fig. 53. *Stoliczkaia* (*Stoliczkaia*) *tenuis* Renz. A-B. Lateral and ventral views of SAM-PCA3169. C-D. Ventral and lateral views of SAM-PCA5475. E. Lateral view of SAM-PCA5476. F. Lateral view of SAM-PCA2939. G-H. Lateral and ventral views of SAM-PCA2938. I. Lateral view of SAM-PCA3373. A-B, I $\times 0,75$, C-H $\times 1$.

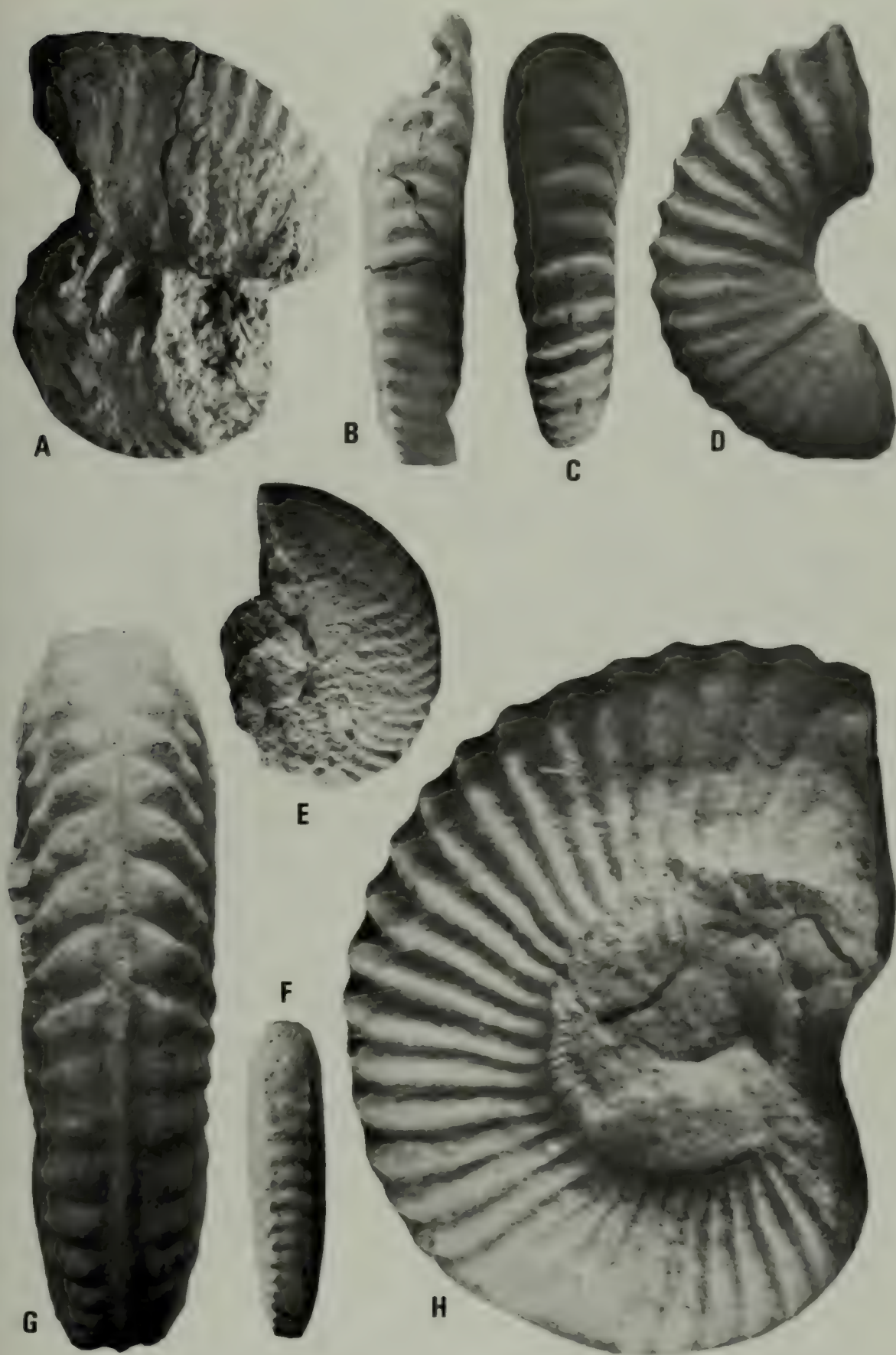


Fig. 54. A-F. *Stoliczkaia (Stoliczkaia) tenuis* Renz. A-B. Lateral and ventral views of SAM-PCA6811. C-D. Ventral and lateral views of SAM-PCA2944. E. Lateral view of SAM-PCA5477. F. Ventral view of SAM-PCA5478. G-H. *Mortoniceras (Angolaites) simplex* (Choffat). Ventral and lateral views of SAM-PCA3107. A-B, E-H $\times 1$, C-D $\times 0.75$.

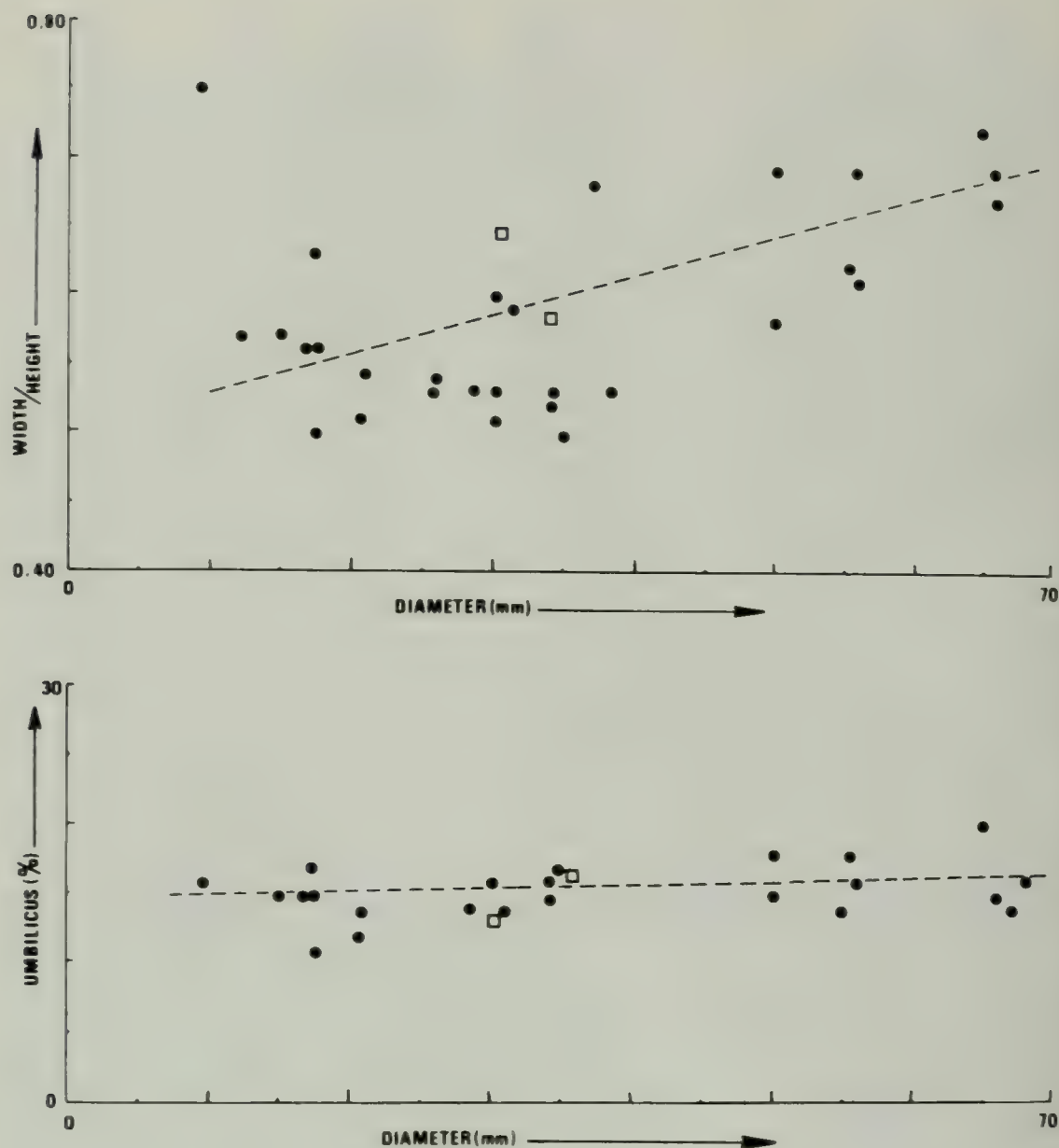


Fig. 55. Plots of inflation and umbilical ratio against diameter for *S. tenuis*. Dots = present material; squares = holotype and paratype (after Renz 1968).

remains are the weak umbilical bulges of the long ribs. Furthermore, the upper half of the flanks are concave, forming a broad, spiral depression.

S. (Stoliczkaia) notha (Seeley) (1865: 232; Spath 1929: 335, fig. 110) (Fig. 57) differs from *S. tenuis* in having a rounded venter at all growth stages. *Stoliczkaia dorsetensis* Spath (1929: 337, pl. 31 (fig. 2), pl. 33 (fig. 1)) is more inflated and more densely ribbed than the Angolan material, as well as having more (three to nine) intercalatories between long ribs on the inner whorls. *S. (Stoliczkaia) villoutreysi* Casey (Fig. 43) has more intercalatories between long ribs (up to seven), whilst the venter is tabulate in maturity, when it homoeomorphs *Hypacanthoplites*.

S. (Stoliczkaia) argonautiformis (Stoliczka) (1864: 87, pl. 46 (figs 1–2)) has strongly converging flanks, subdued ribbing and a more narrowly arched venter than the present species. *Stoliczkaia tetragona* Neumayr (nom. nov. pro *Ammonites dispar* Stoliczka (*non* d'Orbigny), 1864: 85, pl. 45 (fig. 2)) (Fig. 58) differs from the Angolan material in being much more inflated, although the style of ornament is similar in adults.

Stoliczkaia grandidieri Boule, Lemoine & Thévenin (1907: 34, pl. 8 (fig. 8)), *S. gardonica* (Herbert & Meunier-Chalmas) (1875: 116, pl. 4 (figs 1–2)); *S. rhamnonota* (Seeley) (1865: 233, pl. 11 (fig. 7); Spath 1929: 333, fig. 109)) and *S. blancheti* (Pictet & Campiche) (1859: 188, pl. 23 (figs 2, 6); Renz 1968: 46, pl. 5 (fig. 21)) are all referable to the subgenus *Faraudiella*, whilst *S. africana* Pervinquière (1907: 388, pl. 12 (fig. 10)), *S. flexicostata* Breistroffer (nom. nov. pro *A. dispar* Pictet & Campiche (*non* d'Orbigny) 1860: 264, pl. 38 (fig. 4); Renz 1968: 49, pl. 6 (fig. 9)), *S. hashimotoi* Matsumoto & Inoma, and *S. asiatica* Matsumoto & Inoma (1975) are all *Shumarinaia*.

As suggested by Matsumoto & Inoma (1975), *Stoliczkaia uddeni* Böse (1927: 211, pl. 4 (figs 12–15)), is probably a synonym of *S. texana* Cragin (1893: 235, pl. 44 (fig. 1)) which itself is a close relative of *S. crotaloides* (Stoliczka) (1864: 88, pl. 46 (fig. 3)) (Fig. 59). The latter species differs from the Angolan material in maintaining single prorsiradiate ribs to the peristome, with only rare intercalatories, and in the flattened venter of the inner whorls; they may represent a distinct Cenomanian offshoot.

'*Stoliczkaia*' *razafimbelo* Collignon (1968: 29, pl. 6 (fig. 7), pl. 7 (fig. 4)) and '*S.*' *vendegiesi* Collignon (1968: 31, pl. 7 (fig. 5)) both differ from the present material in the development of distinct upper and lower ventrolateral tubercles on the body chamber and are thus transitional to *Graysonites*. They do not appear to be referable to the genus *Stoliczkaia*.

Stoliczkaia patagonica Stoyanow (1949: 128, pl. 26 (figs 3–4)), *S. excentrum-bilicata* Stoyanow (1949: 129, pl. 26 (figs 5–6)) and *S. scotti* Stoyanow (1949: 129, pl. 26 (figs 7–8)) are all from the same stratigraphic level and locality and it is doubtful whether more than one species is represented. In this material, flexuous main ribs are ornamented with umbilical bullae and separated by two to four intercalatories. The ribs pass strongly across the venter and appear to lack ventrolateral tubercles. These 'species' are very close to *S. dorsetensis* Spath.

Stoliczkaia adkinsi Böse (1927: 193, pl. 18 (figs 9–17)) differs from the present material in having more strongly differentiated long and short ribs, the former with distinct umbilical tubercles.

'*Submantelliceras*' *worthense* (Adkins) (1920: 93, pl. 1 (figs 11–13)) from the Pawpaw Formation of Tarrant County, Texas, may be based upon juveniles of *Stoliczkaia*. It differs from the present material in the possession of umbilical tubercles and in the (?) earlier loss of ventrolateral tubercles.

Some of the *Mantelliceras* (*Submantelliceras*) *saxbii* (Sharpe) figured by Thomel (1972: 16–17, pl. 1 (figs 8–12 only)) are clearly based upon *Stoliczkaia*

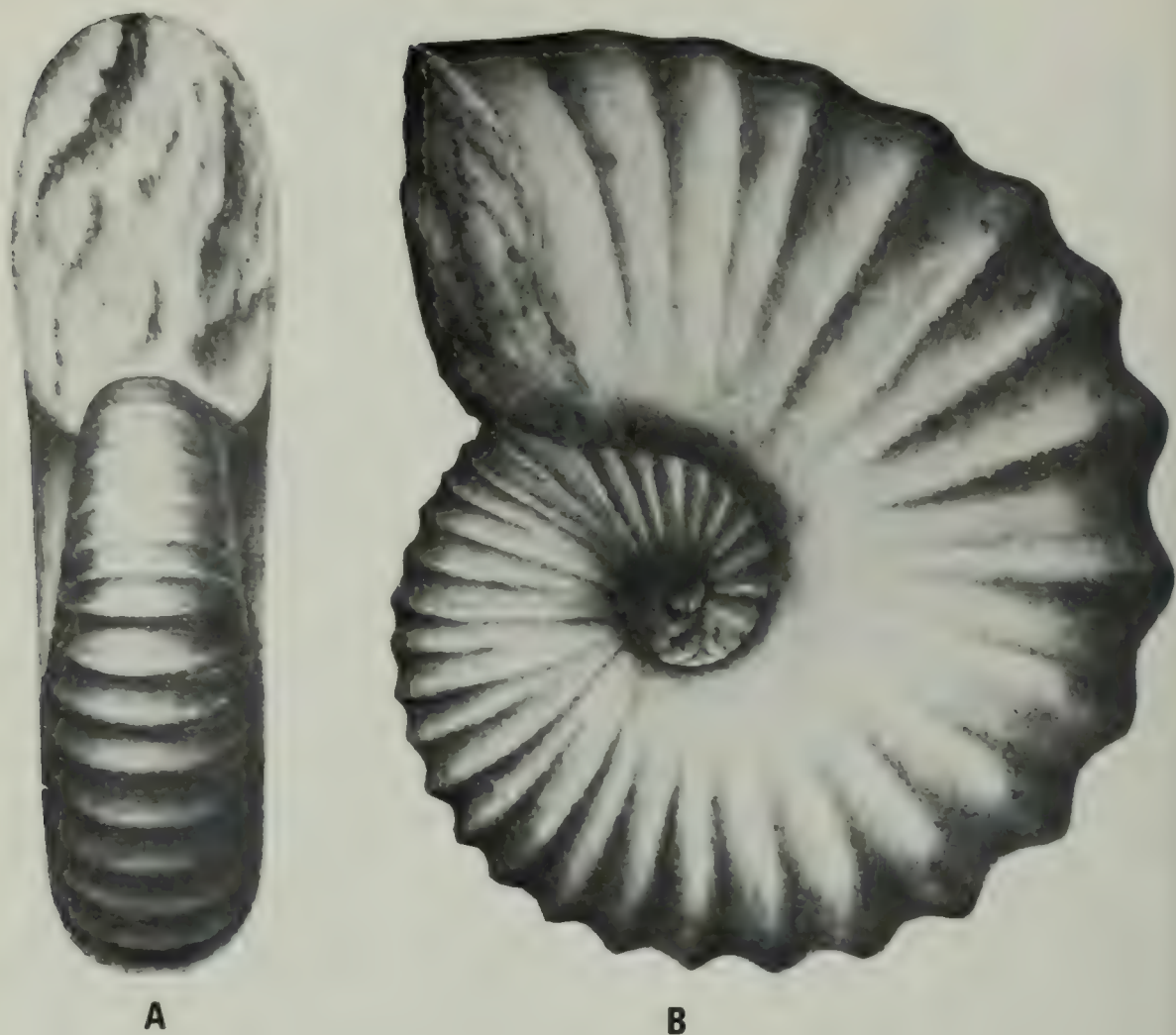


Fig. 56. *Stoliczkaia (Stoliczkaia) clavigera* Neumayr. Copy of Stoliczka 1864, pl. 45 (fig. 1-1a).
×1.

of the *dispar-dorsetensis* group and differ from the Angolan material in having more intercalatories between long ribs.

Stoliczkaia praecursor Anderson (1958: 246, pl. 12 (fig. 1)) is too poorly figured and described for proper comment, but appears to differ from the present species in being more inflated, more coarsely ribbed, and in the presence of umbilical bullae at large diameters. It seems to be allied to *S. tetragona* Neumayr.

In his original account of this species, Renz compared *S. tenuis* with *Mantelliceras martimpreyi* (Coquand), and, indeed, as demonstrated by the present population *S. (S.) tenuis* confirms that some *Stoliczkaia* have sub-mantellicerine nuclei, as suggested by Kennedy (1971). In particular, the authors are impressed by their close similarity to pyritic nuclei such as those figured by Collignon (1929, pl. 3 (figs 4-5)) from Diego-Suarez, Madagascar, as *Acanthoceras (Mantelliceras) martimpreyi* Coquand. The latter differ only in having

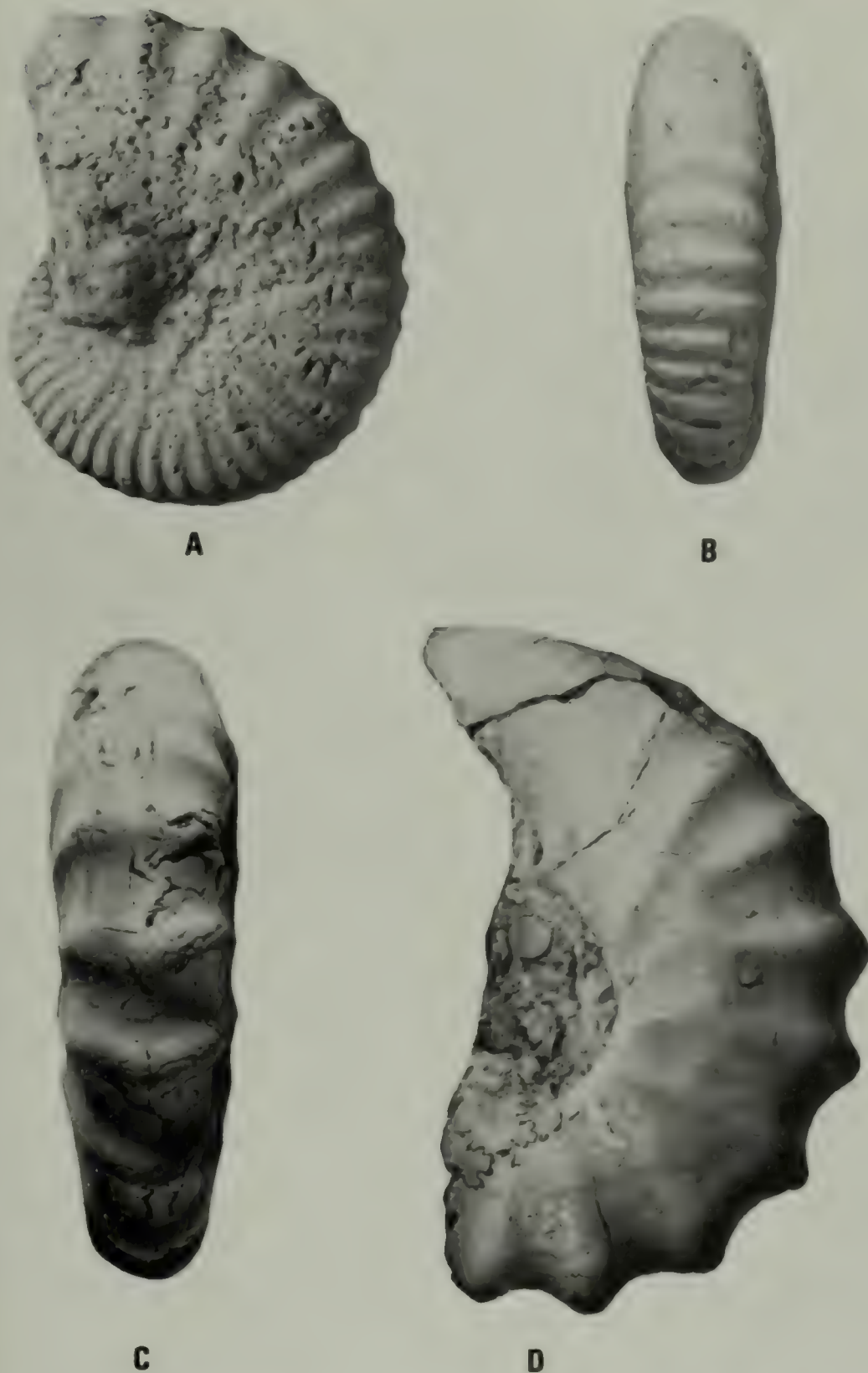


Fig. 57. *Stoliczkaia* (*Stoliczkaia*) *notha* (Seeley). A-B. Holotype, Sedgwick Museum, Cambridge, B40. C-D. BMNH C4811, type of the variety *ultima* Spath. Both from the Cambridge Greensand, Cambridge. $\times 1$.

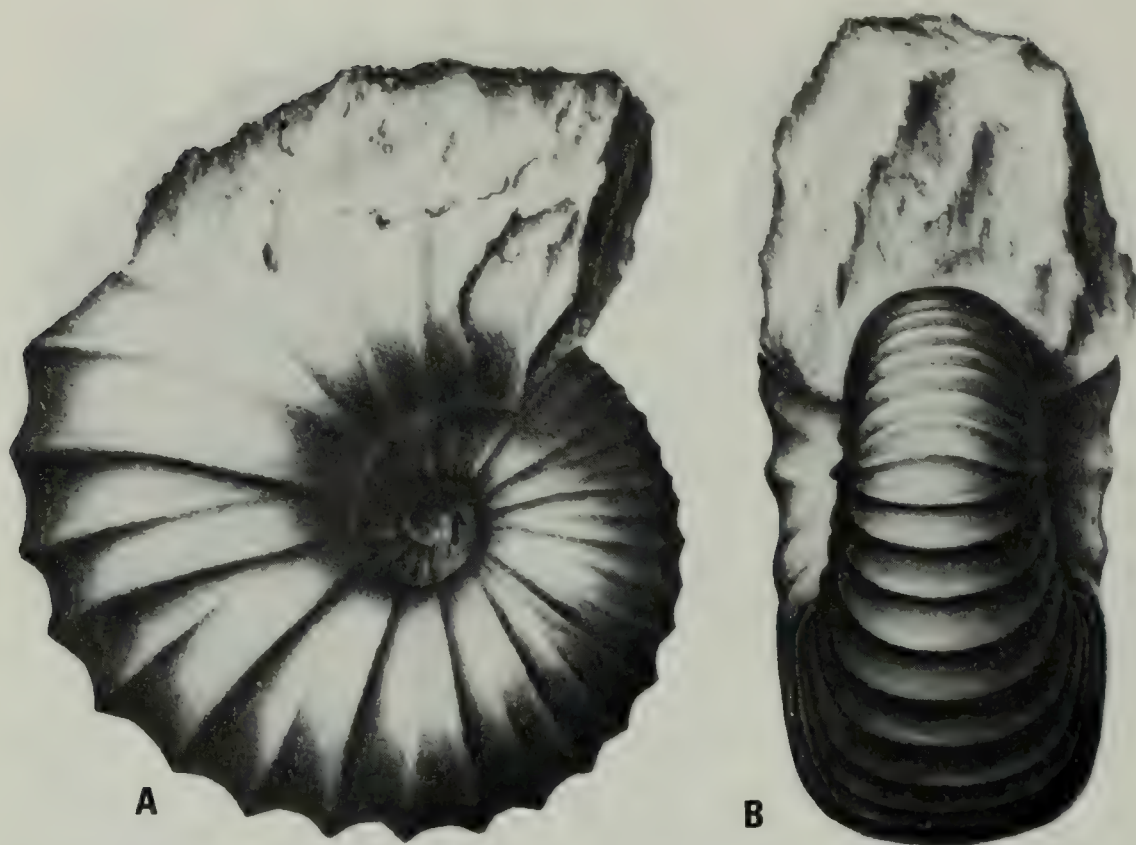


Fig. 58. *Stoliczkaia tetragona* Neumayr. Copy of Stoliczkaia 1864, pl. 45 (fig. 2-2a). $\times 1$.

distinctly differentiated lower ventrolateral tubercles. However, there can be little doubt that records of *Mantelliceras* (Thomel 1972) and *Submantelliceras* (Adkins 1920) from the Upper Albian are based upon juveniles of *Stoliczkaia*. Kennedy & Hancock (1971) have shown *Submantelliceras martimpreyi* (Coquand) to be a junior subjective synonym of *M. saxbii* (Sharpe), from which the authors' material differs in being more compressed, lacking distinct lower ventrolateral tubercles and in showing a marked, and characteristic, change of ornament on the body chamber. However, the fact that Thomel (1972) assigned late Albian species of *Stoliczkaia* to *M. saxbii* merely serves to emphasize the close relationship between these two genera and suggests that the origin of (at least) compressed *Mantelliceras* and *Utaturiceras* lies close to *Stoliczkaia* of *tenuis* type. The writers would also point to the close similarity of compressed variants to juvenile *Forbesiceras* (see Juignet & Kennedy 1977), generally described as *Neopulchellia* (a subjective synonym), and evidence for the descent of *Forbesiceras* from the *S. (S.) tenuis* group is to be published elsewhere.

Occurrence

S. (Stoliczkaia) tenuis is so far known only from the Upper Albian of Switzerland and Angola.

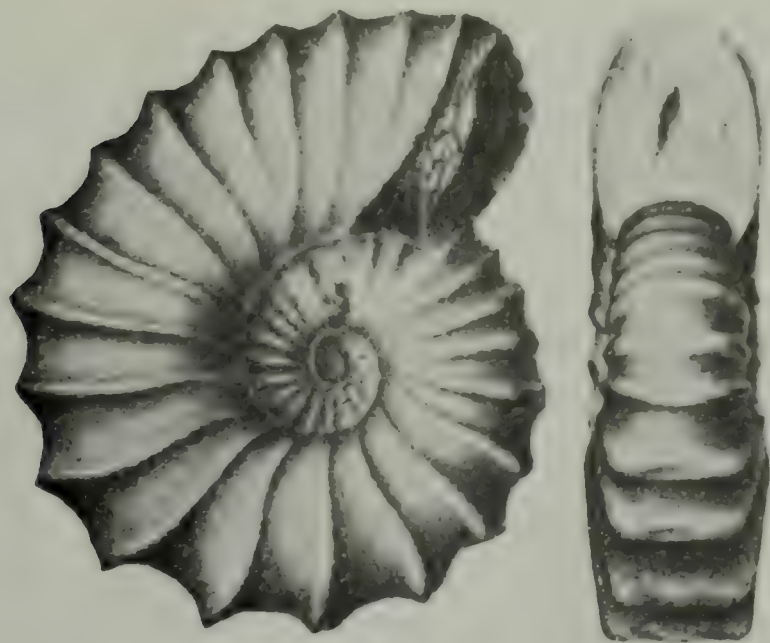


Fig. 59. *Stoliczkaia crotaloides* (Stoliczka). Copy of Stoliczka 1864, pl. 46 (fig. 3–3a).
×1.

Family **Brancoceratidae** Spath, 1934

Subfamily **Brancoceratinae** Spath, 1934

Genus *Hysterocheras* Hyatt, 1900

Type species *Ammonites varicosus* J. de C. Sowerby, 1824

Discussion

Hysterocheras is typically a low Upper Albian micromorph genus, clearly descended from the earlier *Brancoceras*, and has generally been regarded as characteristic of, and largely confined to, the *Mortoniceras inflatum* Zone. However, micromorph brancoceratids persist into the highest levels of Albian where they have generally been referred to as *Spathiceras* or *Mortoniceras* (*Cantabrigites*).

Whitehouse (1927: 110) introduced *Spathiceras* without formal diagnosis, merely naming as type of the genus *Hystrichoceras antipodeum* Etheridge (1902: 47, pl. 7 (figs 6–7)). The holotype of *S. antipodeum* is from the Upper Albian of Point Charles, near Darwin, Northern Australia, where it occurs associated with *Desmoceras latidorsatum* (Michelin) (= *D. carolensis* Etheridge 1902, pl. 7 (figs 2–5)), *Idiohamites* cf. *spinulosus* (J. Sowerby) (= *Ancyloceras* (?) sp. ind., Etheridge 1902, pl. 7 (figs 14–15)), *Scaphites eruciformis* Etheridge (very close to *S. simplex* Jukes-Browne), *Hamites* cf. *virgulatus* (Brongniart) (= *Hamites* (?) sp. ind., Etheridge 1902, pl. 7 (figs 12–13)), *Aucellina gryphaeoides* (J. de C. Sowerby) (= *A. incurva* Etheridge), together with the genera *Beudanticeras*, *Labeceras*, *Myloceras*, *Anisoceras* and *Ptychoceras* (Whitehouse 1928). Because



Fig. 60. *Hysterocheras?* spp. juv. A-B. USNMNH 237018. C-E. USNMNH 237017. F. *Hysterocheras?* cf. *ootatoorensis* (Stoliczka), USNMNH 237016. G-H, K-Z. *Hysterocheras antipodeum* (Etheridge), a series of limonitic specimens from northern Australia. G-H. BMNH C26539. K-L. BMNH C26551. M-N. BMNH C26523. O-Q. BMNH C26552. R-T. BMNH C26548. U-V. BMNH C26518. W-X. BMNH C26546. Y-Z. BMNH C35269. I-J. *Hysterocheras?* *ootatoorensis* (Stoliczka). Copy of Stoliczka 1865, pl. 32 (fig. 2). All $\times 1$.

Whitehouse (1928: 279) considered the fauna to be '... typical of the *substuderi* Zone of the Upper Albian', the name *Spathiceras* has been applied to all flat-sided, weakly tuberculate micromorph mortoniceratinids of uppermost Albian age. However, the genera *Labeceras*, *Myloceras* and *Beudanticeras* are nowhere known to range above the *Mortoniceras inflatum* Zone, and the faunas recorded by Etheridge (1902) and Whitehouse (1927) seem to be typical low Upper Albian (approximately *varicosum* Subzone) assemblages. It is, perhaps, not coincidental, therefore, that *S. antipodeum* (Fig. 60K–Z) bears a remarkable resemblance to *Hysterocheras* of the *binum-subbinum* group, from which it differs only in being consistently more evolute (umbilicus 40–45% of the diameter). The differences are not sufficient for generic separation, and *Spathiceras* is considered a junior subjective synonym of *Hysterocheras*. There is no good evidence for Cenomanian occurrences of the genus.

We are left, therefore, only with *Hysterocheras* for those uppermost Albian mortoniceratinid micromorphs with an evolute shell, and undivided ventrolateral tubercles. Either these represent a continuation of the *Hysterocheras* stock, or they represent an unnamed homoeomorphic development. Until better and larger collections are known, the authors prefer to follow Renz (1968) and refer their material to *Hysterocheras*.

Hysterocheras? cf. *ootaturense* (Stoliczka, 1865)

Fig. 60E–F, I–J

Compare

Ammonites ootaturensis Stoliczka, 1865: 56, pl. 32 (fig. 2).

Mortoniceras ootaturense (Stoliczka) Pervinquier, 1910: 64, pl. 6 (figs 2–5).

Spathiceras ootaturense (Stoliczka) Spath, 1934: 444, 445, fig. 160h. Breistroffer, 1940: 75.

? *Pervinquieria* (?) sp. nov. Breistroffer, 1940: 75.

Material

A single specimen, USNMNH 237016, with recrystallized shell preserved, although somewhat corroded, from Porto Amboim.

Description

Shell small, evolute, with a wide, shallow umbilicus, steep umbilical walls and evenly rounded umbilical shoulder. The whorl section is subquadrate, compressed with flattened flanks. Ribbing is very weak on the inner flank, but strengthens markedly over the ventrolateral shoulder, whilst there is a prominent keel.

Discussion

Stoliczka's (1865) type (Fig. 60I–J) comes from a locality 'near Odium', from where he also records other typical uppermost Albian species such as *M. (Mariella) bergeri* (Brongniart), *M. (M.) circumtaeniatus* (Kossmat),

Anisoceras perarmatum Pictet & Campiche, *D.* (*Desmoceras*) *latidorsatum* (Michelin), and *Lechites gaudini* (Pictet). *Ammonites ootaturense* is probably, therefore, of latest Albian age, although Stoliczka's record of *Turrilites costatus* Lamarck and *Neoptychites xetra* (Stoliczka) from the same locality suggests the presence of beds as high as the Lower Turonian in the vicinity.

Hysterocheras antipodeum (Etheridge) (Fig. 60G–H, K–Z) differs from the Angolan specimen in being somewhat older, with a wider umbilicus, flatter flanks and more prominent umbilical tubercles. The specimen of *Schloenbachia rostratus* var. *antipodeus* (Etheridge) figured by Etheridge (1909, pl. 67 (figs 3–4)) (*non* Etheridge 1902) was referred to *Dipoloceras bouchardianum* (d'Orbigny) by Stieler (1920), but was renamed *Prohysterocheras richardsi* var. *nitidum* by Whitehouse (1926). However, Etheridge's specimen appears indistinguishable from *Dipoloceras quadratum* Spath (1921: 278, pl. 25 (fig. 3)).

Hysterocheras? *nanum* Renz (1968: 63, pl. 11 (fig. 4), fig. 22c–d) differs from *H?* *ootaturense* in having prominent umbilical tubercles at an early stage. The specimen of *H. semileve* Haas recorded by Renz (1968: 63, pl. 11 (fig. 6), fig. 22g–h) from the 'Unteren Vraconnien' appears to be based upon a larger fragment of his *H.?* *nanum*.

Hysterocheras? *tunisiense* (Spath) (nom. nov. pro *Mortoniceras inflatum* var. *orientalis* (?) Pervinquier (non Kossmat) 1907: 229, pl. 11 (fig. 2)) differs from *H?* *ootaturense* and the present specimen in having sharp, flexuous prorsiradiate ribs which bifurcate from distinct umbilical bullae at only 17 mm diameter.

Hysterocheras? *wenoense* (Adkins) (1928: 229, pl. 20 (fig. 13)) differs from the authors' material in its sharp ribbing and distinct umbilical tubercles. The specimen figured by Renz (1968: 62, pl. 11 (fig. 5)) as *Hysterocheras* cf. *subbinum* Spath may possibly belong here.

'*Algericeras*' *boghariense* (Coquand) (Pervinquier 1907: 240, pl. 11 (fig. 16)) differs from the present specimen in having a quadrate whorl section ($W/H = 1.00$) with dense, fine, straight ribs, about thirty-two per half whorl, which arise in pairs from umbilical bullae and terminate in ventrolateral tubercles. It is said to be of Cenomanian age but appears merely to be based upon pyritic nuclei of *Mortoniceras*.

Occurrence

Hysterocheras? *ootaturense* is known from the Upper (? uppermost) Albian of southern India, and possibly the uppermost Albian of France, Algeria and Angola.

Subfamily Mortoniceratinae Spath, 1925

Genus *Mortoniceras* Meek, 1876Subgenus *Durnovarites* Spath, 1932Type species *Subschloenbachia perinflata* Spath, 1921*Discussion*

Wiedmann & Dieni (1968: 142) have divided the subgenus *Durnovarites* into two species groups:

1. The group of *M. (D.) subquadratum*, characterized by four rows of tubercles on the ribs. To this group may be assigned *M. (D.) subquadratum* Spath, *M. (D.) quadratum* Spath, *M. (D.) perinflatum* (Spath), *M. (D.) postinflatum* Spath, *M. (D.) depressum* (Spath), *M. (D.) adkinsi* (Young), *M. (D.) vraconense* Renz, *M. (D.) spinosum* (van Hoepen non Pervinquierè), *M. (D.) subnanum* (Breistroffer), *M. (D.) ishiguaense* Reyment, *M. (D.) levecostatum* Reyment, *M. (?D.) crassicornutum* (Reyment), *M. (D.) lowrii* McLearn, *M. (D.) downii* McLearn, *M. (D.) rerati* Collignon and *M. (D.) haueri* Collignon.
2. The group of *M. (D.) spinosum*, with only three rows of tubercles and subordinate ribbing (appears merely to be based upon juveniles which have still to develop the fourth row of tubercles). To this group belong *M. (D.) spinosum* (Pervinquierè), *M. (D.) kentronotum* Spath, *M. (D.) lemoinei* (Spath), *M. (D.) neokentroides* Wiedmann & Dieni and *M. (D.) aubersonense* Renz.

Mortoniceras (Durnovarites) perinflatum (Spath, 1922)

Figs 3G, 61, 62D–I, 63–64

Ammonites inflatus Pictet & Campiche (non J. Sowerby), 1860: 178, pl. 21 (fig. 5), pl. 22 (fig. 3).

Inflaticeras ('*Subschloenbachia*') *perinflatum* Spath, 1922: 113.

? *Inflaticeras* (*Subschloenbachia*) *depressum* Spath, 1922: 114, figs B, 2a–d.

Inflaticeras (*Subschloenbachia*) *quadratum* Spath, 1922: 115.

Pervinquieria quadrata (Spath) Spath, 1926b: 423.

? *Pervinquieria depressa* (Spath) Spath, 1928: 51.

Mortoniceras (Durnovarites) perinflatum (Spath) Spath, 1933: 430, pl. 40 (fig. 2), fig. 150.

Wiedmann & Dieni, 1968: 143, pl. 14 (figs 3–4), fig. 92. Renz, 1968: 51, pl. 8 (figs 3, 5, 8), pl. 9 (figs 1–2), figs 17a, 18c, 19c, f. Marcinowski & Naidin, 1976: 109, pl. 6 (figs 1–2).

Mortoniceras (Durnovarites) quadratum (Spath) Spath, 1933: 432, pl. 45 (fig. 3), pl. 46 (fig. 6), pl. 49 (fig. 12). Reyment, 1955: 38, pl. 6 (figs 4–5), pl. 7 (fig. 3), fig. 15. Wiedmann & Dieni, 1968: 145, fig. 93.

Mortoniceras (Durnovarites) postinflatum Spath, 1933: 433, pl. 40 (figs 3–5), pl. 46 (figs 3, 7), pl. 47 (fig. 6). Renz, 1968: 53, pl. 8 (figs 1–2, 6), figs 17b, d, 18b, 19a–b, d. Marcinowski & Naidin, 1976: 109, pl. 7 (fig. 1), pl. 8 (fig. 1).

? *Mortoniceras (Durnovarites) depressum* (Spath) Collignon (in Besairie), 1936: 195. Reyment, 1955: 37, pl. 7 (fig. 4), fig. 14.

Durnovarites adkinsi Young, 1957: 6, pl. 1 (figs 3, 6).

Mortoniceras (Durnovarites) vraconense Renz, 1968: 54, pl. 7 (figs 6–7, 11), fig. 19e. Marcinowski & Naidin, 1976: 111, pl. 9 (fig. 1).

Material

Two specimens, USNMNH 237021–22, both with recrystallized shell preserved from Porto Amboim, together with three specimens, SAM-PCA4802, 4576 and 4587, from Cabo Ledo.



Fig. 61. *Mortoniceras* (*Durnovarites*) *perinflatum* (Spath). The holotype, Pictet collection, Natural History Museum, Geneva. From the Upper Albian of Vraconne, Switzerland. $\times 1$.

Description

The shell is moderately inflated and rather evolute (umbilicus 32–36% of the diameter), with a wide, shallow umbilicus and steep umbilical walls. The whorl section is almost quadrate ($W/H = 0,93-1,05$), with subparallel flanks. The umbilical shoulder is evenly rounded intercostally. Ribs begin at the umbilical seam and are rectiradiate to the umbilical shoulder where they terminate in weak bullae. The latter give rise to 1–2 prorsiradiate flank ribs, 38–43 per whorl and broader than the interspaces. All ribs are ornamented by a midlateral tubercle and closely spaced upper and lower ventrolateral tubercles. On the venter, the ribs pass forwards, finally becoming effaced in the sulci bordering the siphonal keel. The ribs show spiral ornament which is especially prominent on the ventrolateral tubercles.

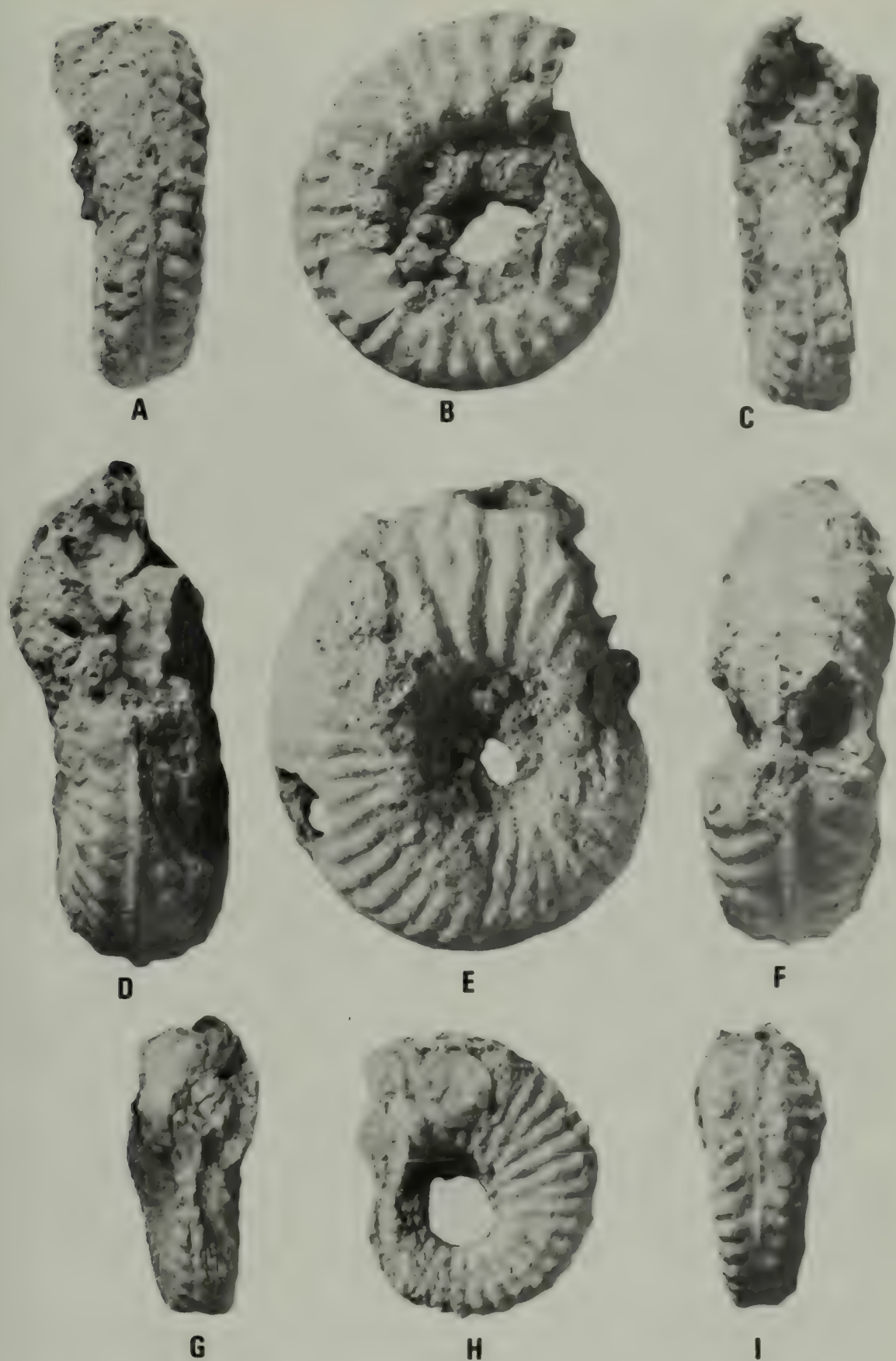


Fig. 62. A-C. *Mortoniceras* (*Durnovarites*) *subquadratum* Spath, USNMNH 237023. D-I. *Mortoniceras* (*Durnovarites*) *perinflatum* (Spath). D-F. USNMNH 237021. G-I. USNMNH 237022. $\times 1$.

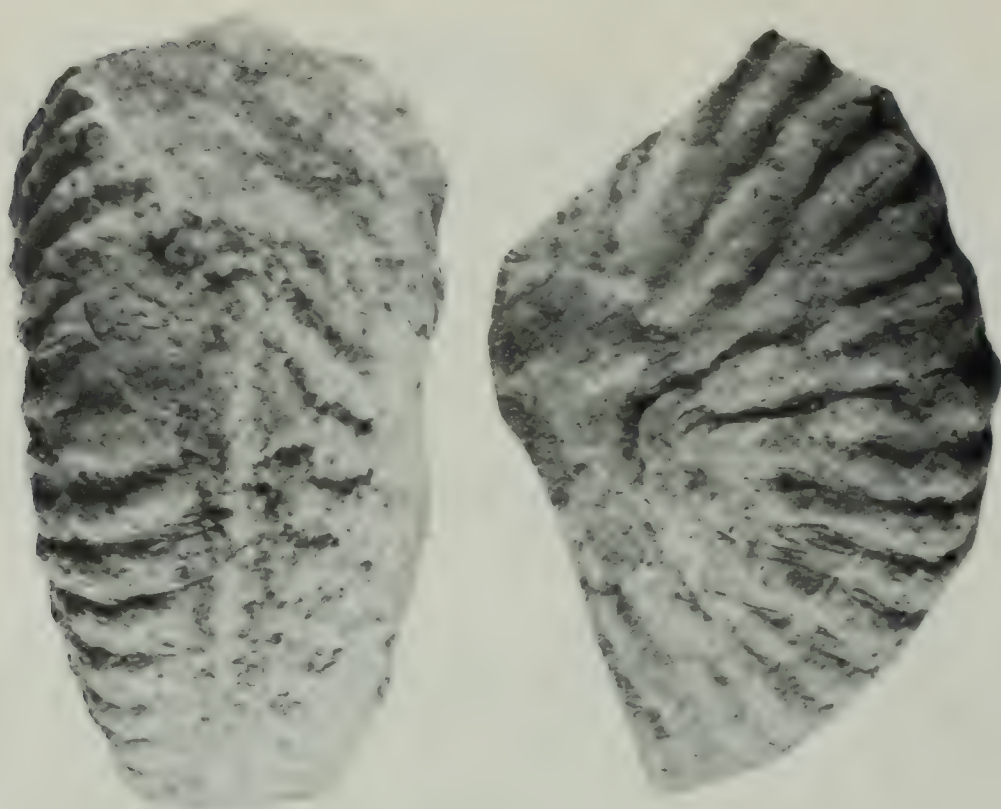


Fig. 63. *Mortonicerias* (*Durnovarites*) *perinflatum* (Spath). Ventral and lateral views of SAM-PCA4802. $\times 1$.

Measurements

No.	D	H	W	w/H	U
USNMNH 237021	53	22,5(42)	?	?	17(32)
„	44	$\pm 19(43)$	$\pm 20(45)$	1,05	?
USNMNH 237022	35	$\pm 16(46)$	$\pm 15(43)$	0,93	12,5(36)

Discussion

Renz (1968) showed *M. (D.) quadratum* to be based upon juveniles of *M. (D.) perinflatum*, whilst *M. (D.) vracense* appears to comprise hyponodose adults which the authors do not consider to bear specific separation from *M. (D.) perinflatum*.

Similarly, *M. (D.) postinflatum* differs from the strictly contemporaneous *M. (D.) perinflatum* only by its more prominent ventrolateral tubercles and more inflated whorls ($w/H = 1,20-1,65$). The authors do not regard the differences as sufficient for specific separation and place *M. (D.) postinflatum* within the synonymy of *M. (D.) perinflatum*, although the name might usefully be retained at the varietal level.

Durnovarites adkinsi Young was separated from *M. (D.) perinflatum* on the basis of its slightly rounder ribs, less tumid flanks, and denser-ribbed inner

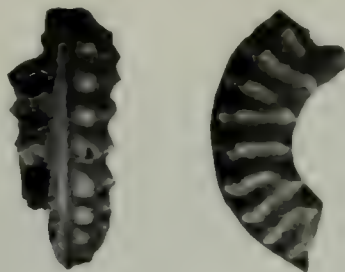


Fig. 64. *Mortonicerias* (*Durnovarites*) *perinflatum* (Spath). The holotype of *Durnovarites spinosus* van Hoepen, SAM-D3154, from the Upper Albian of the Mzinene Formation, Zululand. $\times 1$.

whorls. The differences appear to be those between individuals, and the Texas species is considered to be referable to *M. (D.) perinflatum*.

Mortonicerias (*Durnovarites*) *depressum* (Spath) was said to differ from *M. (D.) quadratum* in its far more depressed whorl section, with rounded instead of parallel flanks. It closely approaches *M. (D.) postinflatum* and may, therefore, be no more than an extreme variant of *M. (D.) perinflatum*.

Occurrence

Mortonicerias (*Durnovarites*) *perinflatum* is known from the uppermost Albian of Switzerland, Poland, southern England, Sardinia, Texas, Nigeria and Angola. The authors have also seen comparable material from Zululand.

Mortonicerias (*Durnovarites*) *subquadratum* Spath, 1933

Figs 62A–C, 65C–D

? *Subschloenbachia meunieri* Spath, 1922: 115.

? *Mortonicerias* (*Durnovarites*) *meunieri* (Spath), Spath 1932: 399.

Mortonicerias (*Durnovarites*) *subquadratum* Spath, 1933: 435, pl. 42 (fig. 5), pl. 43 (fig. 1), pl. 44 (fig. 6), pl. 45 (fig. 5), pl. 47 (figs 2–4), pl. 48 (fig. 2). Reymont, 1955: 38. Dieni & Massari, 1963: 798. Wiedmann & Dieni, 1968: 142, pl. 13 (fig. 9), fig. 90. Renz, 1968: 55, pl. 7 (figs 8, 10), pl. 10 (figs 1–4, 7–8), fig. 17f₁–f₂. Marcinowski & Naidin, 1976: 110, pl. 6 (fig. 3).

Mortonicerias (*Durnovarites*) *subquadratum* var. *tumida* Spath, 1933: 435, pl. 48 (fig. 4). Wiedmann & Dieni, 1968: 143, pl. 13 (fig. 10), fig. 91.

Mortonicerias (*Durnovarites*) *subquadratum* var. *crassicostata* Spath, 1933: 432, pl. 42 (fig. 9).

? *Mortonicerias* (*Pervinquieria*) sp. juv., Spath, 1933: 412, pl. 41 (fig. 7).

? *Pervinquieria* (*Cantabrigites*?) *subnana* Breistroffer, 1947: 91.

Pervinquieria (*Durnovarites*) *subquadrata* (Spath) Breistroffer, 1947: 61.

Durnovarites spinosus van Hoepen, 1951: 324, figs 380–383.

? *Mortonicerias* (*Durnovarites*) *levecostatum* Reymont, 1955: 38, pl. 7 (fig. 2).

? *Mortonicerias* (*Durnovarites*) *subnanum* (Breistroffer) Renz, 1968: 56, pl. 10 (figs 5–6), fig. 17g.

Material

A single specimen, USNMNH 237023, with recrystallized shell preserved from Porto Amboim, and one, SAM-PCA3235, from Praia-Egito, preserved as an internal mould.

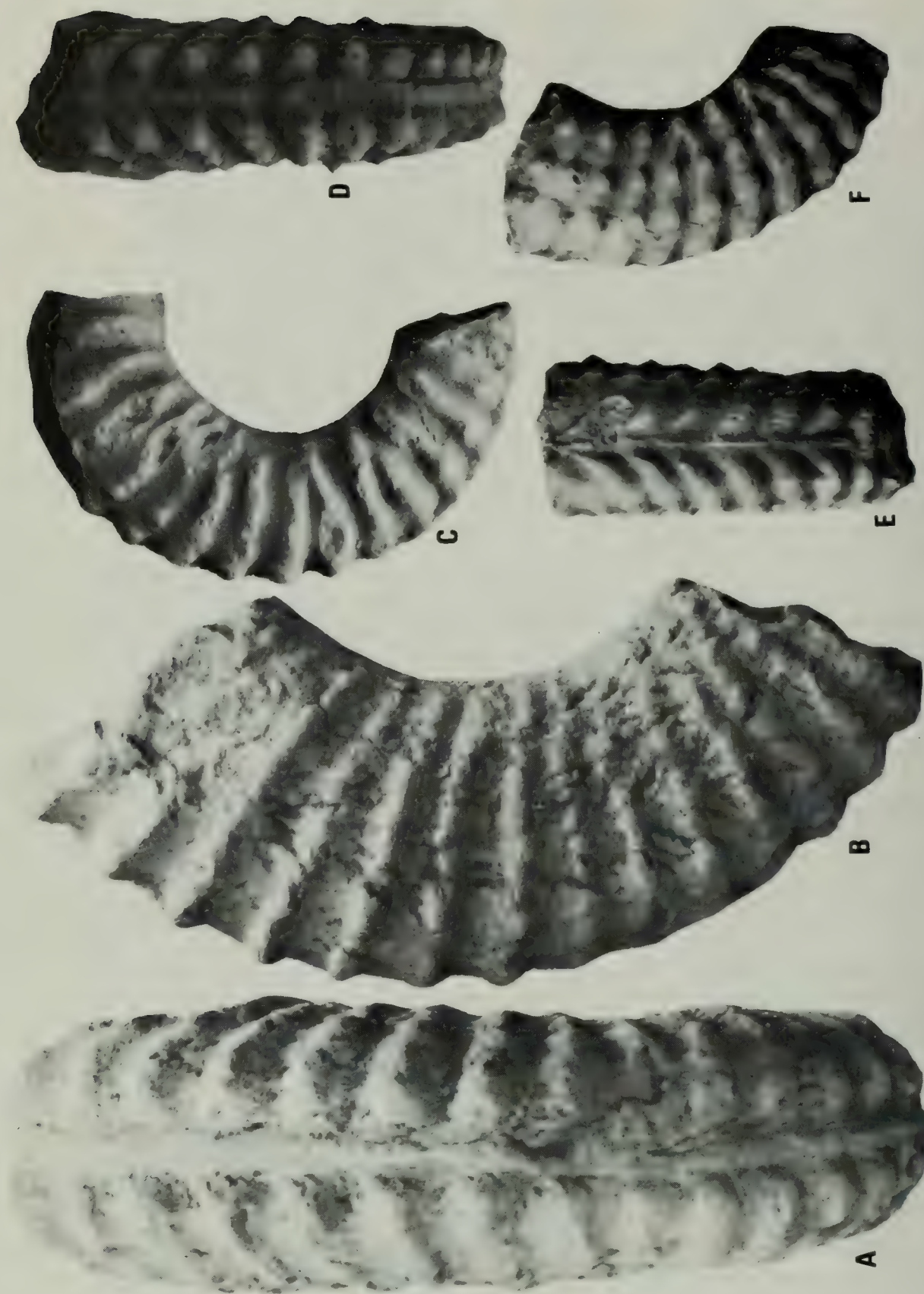


Fig. 65. A-B, *Mortonicerias (Angolaites) simplex* (Choffat). Ventral and lateral views of SAM-PCA3150. C-D, *Mortonicerias (Durnovarites) subquadratum* Spath. Lateral and ventral views of SAM-PCA3235. E-F, *Mortonicerias (Durnovarites) collignoni* sp. nov. Ventral and lateral views of a paratype SAM-PCA3309 $\times 1$.

Description

The shell is very evolute (umbilicus 50% of diameter), compressed, with a slightly depressed, subquadrate whorl section ($W/H = 1,11$). The umbilicus is wide, shallow, with steeply inclined walls and evenly rounded umbilical shoulders. The flanks are flattened, with maximum width close to the umbilical shoulder, and converge slightly to the broad venter.

There are 10 prominent, somewhat bullate umbilical tubercles per half-whorl, from which arise 1–2 rectiradiate to slightly rursiradiate ribs. Where single there is frequently an adjacent intercalated rib, so that there are 19 ribs per half-whorl. The ribs are thick, robust, about as wide as the interspaces, and are ornamented by closely spaced double ventrolateral tubercles. The lower ventrolateral tubercle is sharp and prominent, whereas the upper ventrolateral tubercle is more weakly developed and clavate. On the final third of the outer whorl (which is entirely septate), there is a weakly developed midlateral tubercle. The well-developed siphonal keel is separated from the upper ventrolateral clavi by prominent sulci. The ribs on the adoral portion of the outer whorl show weakly developed spiral ornament.

Measurements

No.	D	H	W	W/H	U
USNMNH 237023	46	13,5(29)	$\pm 15(33)$	1,11	23(50)

Discussion

Mortoniceras (Durnovarites) meunieri (Spath) (1922: 115; 1932: 399) (nom. nov. pro *Ammonites inflatus* Meunier (non J. Sowerby) 1887: 61, pl. 1 (fig. 2)) is an evolute species with about 30 coarse, rectiradiate to slightly rursiradiate ribs arising singly or in pairs from umbilical tubercles, each ornamented with a prominent midlateral tubercle and a (?) double ventrolateral tubercle. Meunier (1888) figured his specimen only in lateral view, without description, and hence comparison is difficult. If it is, indeed, a *M. (Durnovarites)*, then not only might it be a synonym of *M. (D.) subquadratum*, but it also has priority over that name.

This species differs from *M. (D.) perinflatum* (Spath) in its much wider umbilicus (43–50% as against 28–36%) and its typically less depressed whorl section ($W/H = 1,03$ – $1,16$). However, adults of *M. (D.) subquadratum* are unknown and until population studies are undertaken it is not known whether the differences are truly of specific importance.

Renz (1968) included *Durnovarites spinosum* van Hoepen (non Pervinquière) in the synonymy of *M. (D.) subquadratum*, an assignment with which the authors concur; the type is re-illustrated here as Figure 64.

Mortoniceras (Durnovarites) ishiaguense Reymont (1955: 38, pl. 7 (fig. 1)) is very close to *M. (D.) subquadratum* but is apparently much more densely ribbed. Since the Nigerian species is based upon a mature individual, it is not

directly comparable with *M. (D.) subquadratum* at the present time. *Mortoniceras (Durnovarites) levecostatum* Reyment (1955: 38, pl. 7 (fig. 2)) is based upon a somewhat distorted composite internal mould showing about twenty-six coarse, robust ribs per whorl and with a wide umbilicus. Judging from Reyment's (1955) description, it may not bear separation from *M. (D.) subquadratum*.

Occurrence

Mortoniceras (Durnovarites) subquadratum is known from southern England, Poland, Switzerland, Sardinia, Zululand, and Angola.

Mortoniceras (Durnovarites) collignoni sp. nov.

Figs 65E–F, 66–67, 68B–D, 69

Material

About a hundred specimens, in the South African Museum, Cape Town, from Praia-Egito. All are preserved as composite internal moulds.

Type material

SAM-PCA3227 is designated as holotype; paratypes are SAM-PCA2975, 3189, 3199, 3202, 3217, 3259, 3277, 3294, 3309, 3317 and 3407.

Etymology

For the late General Maurice Collignon who contributed so much to our knowledge of ammonite systematics, and who helped the authors with their studies in many ways.

Diagnosis

A densely ribbed species of *M. (Durnovarites)* characterized by a dramatic change in shell morphology on the adult body chamber. The phragmocone has a subrectangular, compressed whorl section and is ornamented with 36–42 rectiradiate to prorsiradiate ribs per whorl which frequently bifurcate from umbilical bullae and are all ornamented with midlateral and double ventrolateral tubercles. On the adult body chamber, however, all tuberculation is rapidly lost and the simple ribs develop a strong convex-adoral curvature, while the whorl section now becomes strongly compressed and lanceolate.

Description

Almost all the material has been crushed to varying degrees.

The coiling is evolute (umbilicus about 24–30% of diameter), with a more or less compressed whorl section from an early growth stage (Fig. 69). Up to the body chamber, the intercostal whorl section is generally subrectangular, compressed. On the body chamber, the flanks become strongly convergent and the whorl section eventually becomes lanceolate. The umbilicus is wide, shallow, with a steep umbilical wall on the inner whorls, and an evenly rounded umbilical shoulder. On the outer whorl, the umbilical wall becomes sloping and the umbilical shoulder is gently rounded.

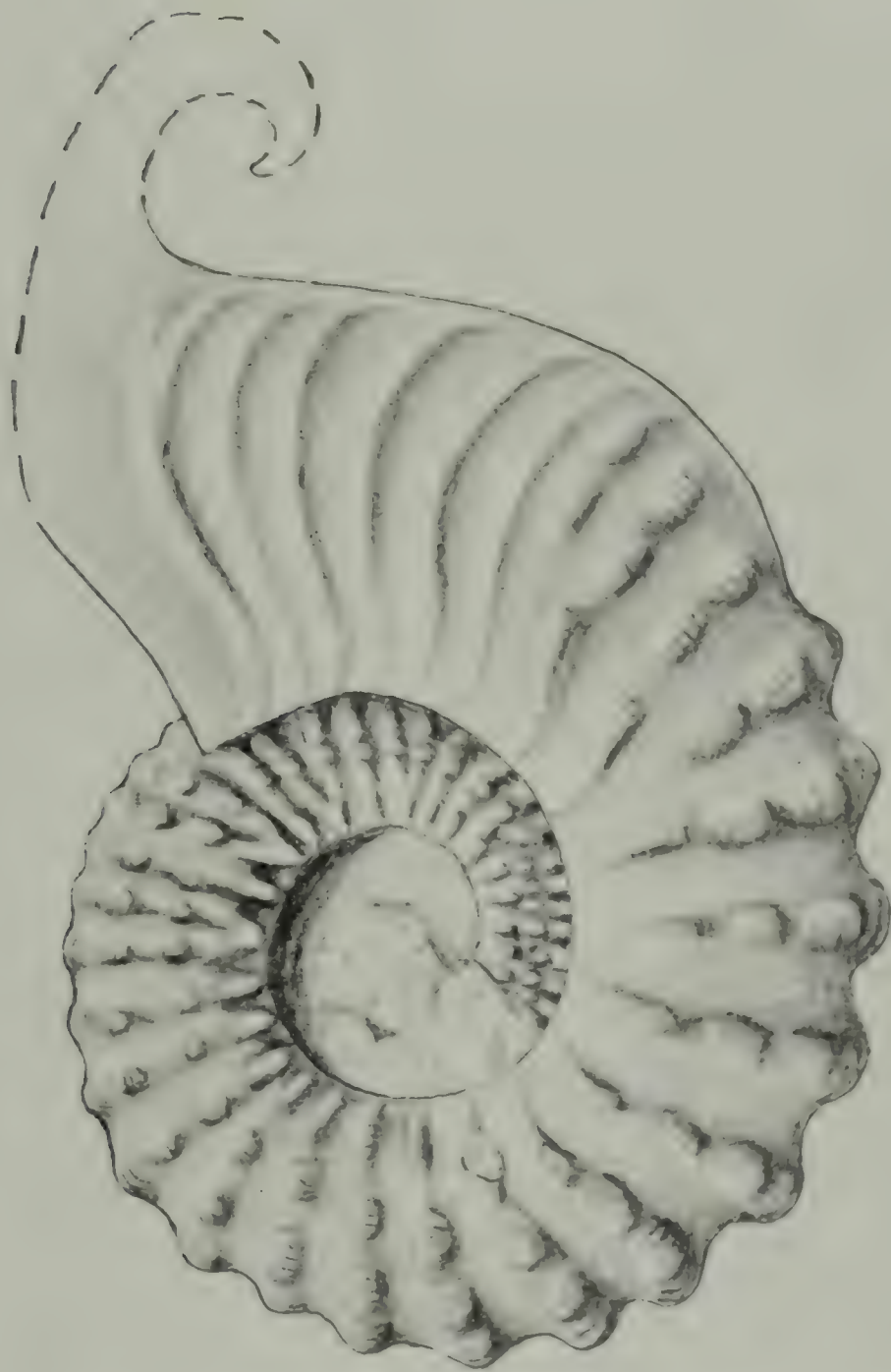


Fig. 66. *Mortoniceras* (*Durnovarites*) *collignoni* sp. nov. A reconstruction based on the holotype and paratype material. $\times 0,66$.

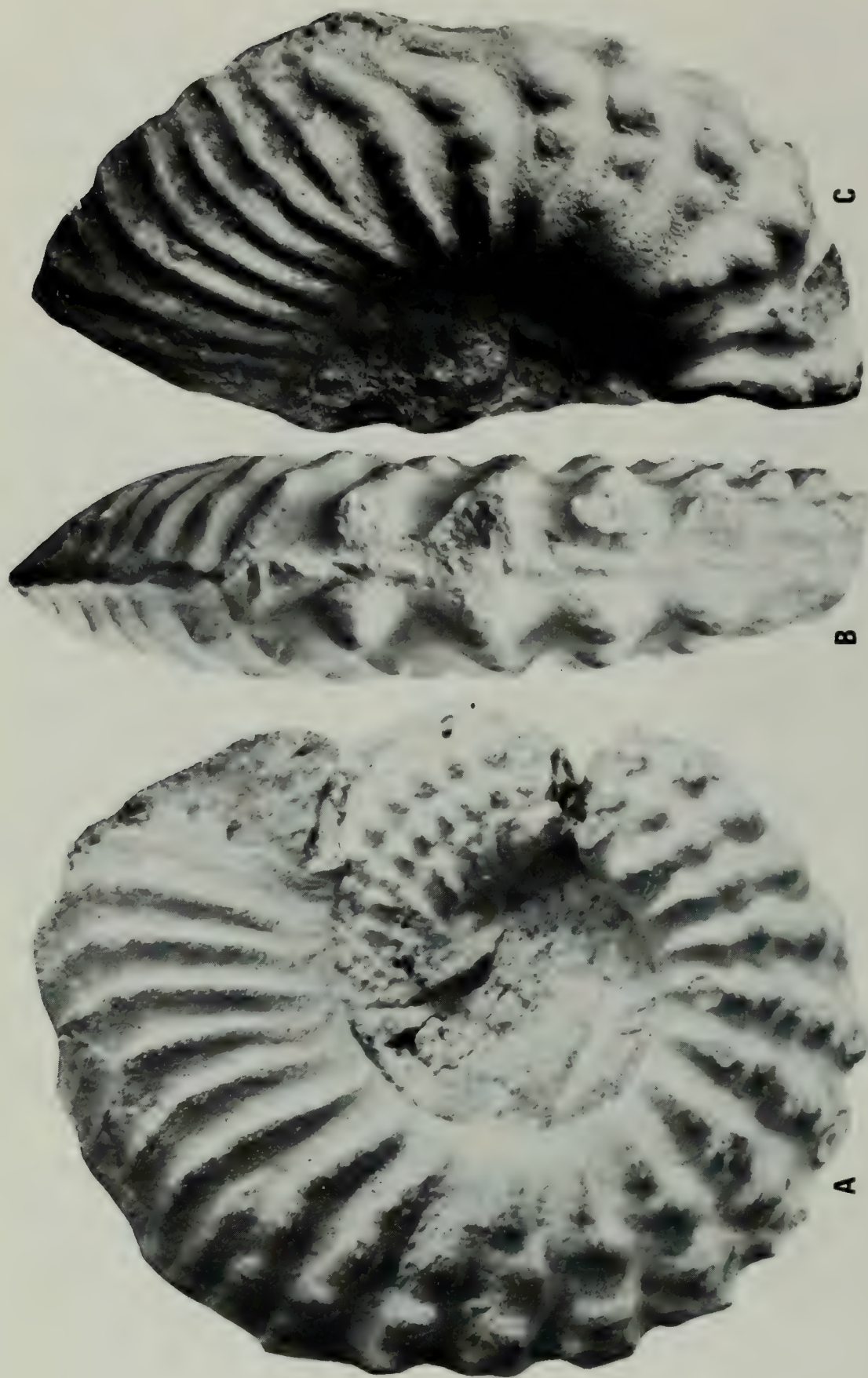


Fig. 67. A-C. *Mortoniceras* (*Durnovarites*) *collignoni* sp. nov. A-B. Lateral and ventral views of the holotype, SAM-PCA3227, C. Lateral view of a paratype, SAM-PCA3278. A-B $\times 0.66$, C $\times 1$.

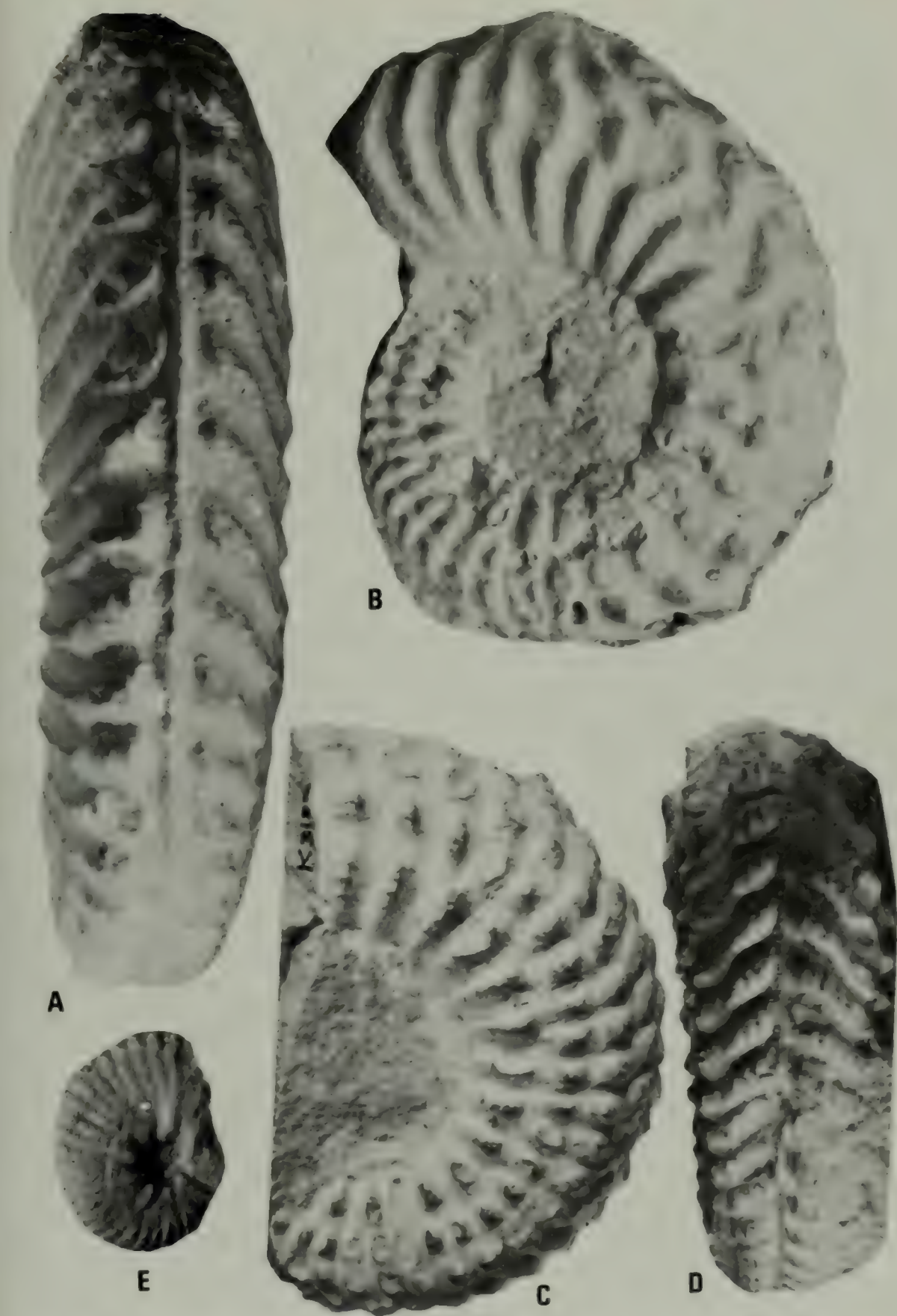


Fig. 68. A. *Mortonicerias* (*Angolaites*) *simplex* (Choffat). Ventral view of SAM-PCA3142. B-D. *Mortonicerias* (*Durnovarites*) *collignoni* sp. nov. B. Lateral view of a paratype, SAM-PCA3269. C-D. Lateral and ventral views of a paratype, SAM-PCA3182. E. *Stoliczkaia tenuis* Renz. Lateral view of SAM-PCA3313. A-B $\times 0,66$, C-E $\times 1$.

In the earliest observed growth stages, the ribbing is generally simple, slightly prorsiradiate, with frequent intercalatories. All ribs are ornamented by distinct lateral and upper and lower ventrolateral tubercles, while long ribs arise from fairly prominent bullae. Even at this stage, spiral notching is evident on the tubercles. In the middle growth stages, the connections between the intercalated ribs and the umbilical bullae strengthen, and many ribs are seen to bifurcate from the latter, while the lateral and upper and lower ventrolateral tubercles become more swollen. At large growth stages, the ribbing again becomes simple but very subordinate to the now very swollen and prominent lateral and ventrolateral tubercles. At this stage, the lower lateral tubercle is somewhat clavate and the upper lateral and ventrolateral tubercles strongly so. The ventrolateral tubercles are now prominently raised above the narrow, sunken, keeled venter. On the last portion of the body chamber there is a great change in ornament. The whorl section changes from subrectangular to lanceolate, with the disappearance of all tubercles, and the ribs become strongly convex.

There are generally 36–42 ribs per whorl in the middle growth stages, about as wide as the interspaces, with somewhat fewer in juveniles and on the outer whorl.

Discussion

The body chamber ornament of this species is characteristic.

Mortoniceras (*Durnovarites*) *perinflatum* (Spath) (Renz 1968: 51, pl. 9 (fig. 1)) differs from *M. (D.) collignoni* sp. nov. in having a strongly depressed whorl section in maturity, whilst *M. (D.) subquadratum* Spath (1933: 435, pl. 37 (fig. 6)) differs from the Angolan species in being more evolute (umbilicus 40–48% of the diameter) and in apparently lacking the dramatic change in body chamber ornament shown by *M. (D.) collignoni*.

Mortoniceras rostratum (J. Sowerby) (Fig. 70) differs from the present species in having sparser, more distant ribbing, whilst the ribs of the body chamber retain four rows of tubercles almost to the peristome.

Mortoniceras (*Durnovarites*) *ishiaguense* Reyment (1955: 38, pl. 7 (fig. 1)) differs from the present species in being more evolute, with less compressed whorls, and in apparently lacking the characteristic change in the body ornament seen in *M. (D.) collignoni*. *Mortoniceras levecostatum* Reyment (1955: 38, pl. 7 (fig. 2)) is from the same locality and horizon as *M. (S.) ishiaguense* but was said to differ in being more distantly ribbed, with more irregular ornament. The differences may not be of specific significance.

Howarth (1965) considered *Neokentroceras curvicornu crassicornutum* Reyment (1955: 41, pl. 4 (figs 7–8)) a species of *Durnovarites*, but Reyment (1955) records this form in association with a typical *N. curvicornu* Spath, and hence it is much older than typical *M. (Durnovarites)*.

Mortoniceras (*Styphloceras*) *lowrii* McLearn (1972: 72, pl. 30 (figs 1–3), pl. 39 (figs 3–4)) and *M. (S.) downii* McLearn (1972: 73, pl. 31 (figs 1–3)) are

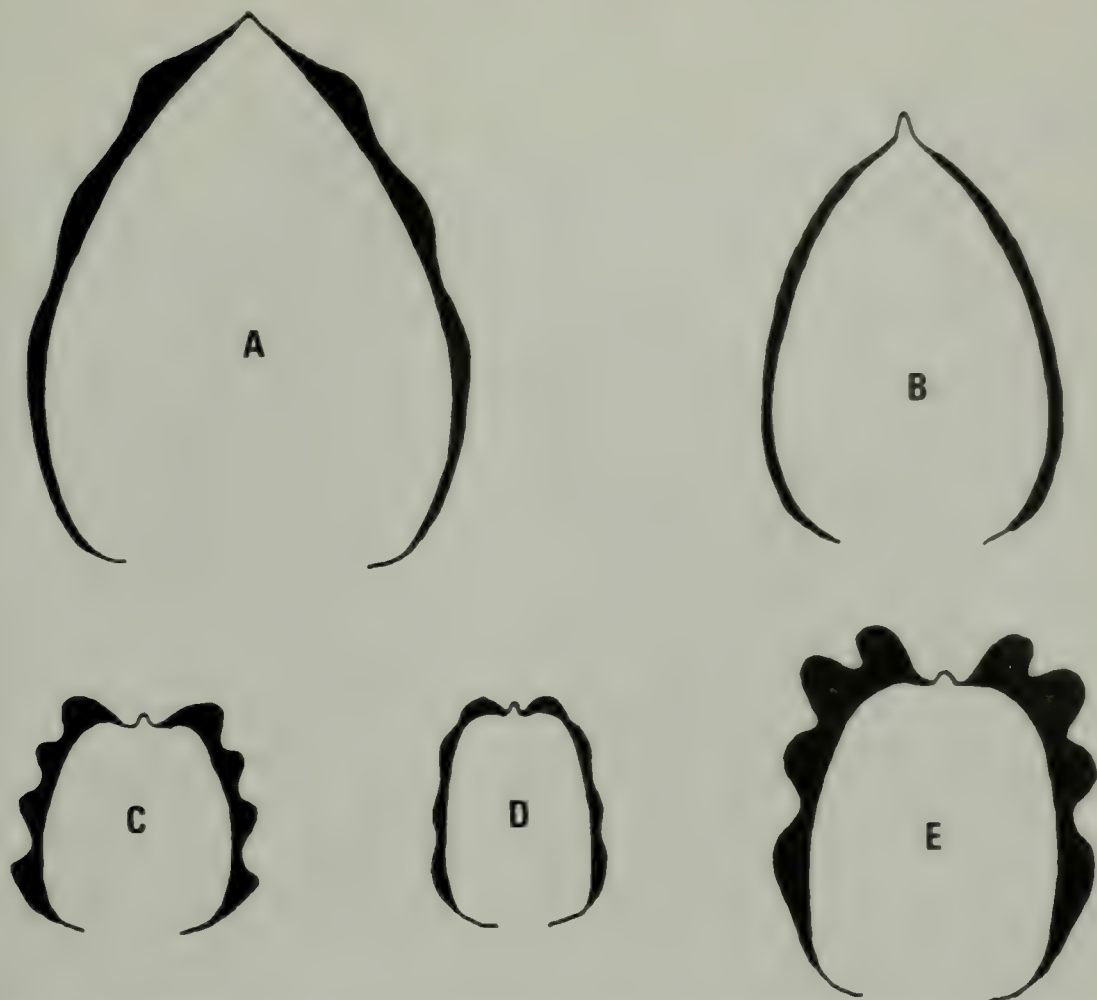


Fig. 69. *Mortonicerias* (*Durnovarites*) *collignoni* sp. nov. Whorl sections. A. SAM-PCA3202. B. SAM-PCA3309. C. SAM-PCA3278. D. SAM-PCA3257. E. SAM-PCA3309. $\times 1$.

both species of *Durnovarites*, thus indicating the presence of uppermost Albian strata at the Skidegate Inlet, British Columbia. *Mortonicerias* (*Durnovarites*) *lowrii* differs from the present species in having very depressed inner whorls, somewhat more distant ribbing, and in lacking the modifications of the body chamber ornament seen in the Angolan species. *Mortonicerias* (*Durnovarites*) *downii* is based upon body chamber fragments. In its swollen, clavate tuberculation it approaches *M. (D.) collignoni*, but it appears to be more inflated, and shows no sign of the body chamber becoming lanceolate.

Mortonicerias (*Durnovarites*) *depressum* (Spath) (1922: 114, figs B, 2a-d) is based upon a body chamber fragment of a specimen about 50 mm in diameter. At this stage, the whorls are very depressed ($W/H = 1.41$) and the fragment appears to have been very evolute. Slightly prorsiradiate ribs arise from prominent umbilical bullae and are indistinctly bifurcating, so as to appear alternating long and short. There are four rows of tubercles, with maximum width at mid-flank. This species would seem to be closely allied to *M. (D.) subquadratum* var. *tumidum* Spath; it differs from the Angolan material in being



Fig. 70. The holotype of J. Sowerby's *Ammonites rostratus*, from the Upper Greensand of Roak, near Benson, Oxfordshire. Oxford University Museum K835. $\times 0,75$.

more coarsely ribbed and (?) more evolute, with a strongly depressed whorl section.

Mortoniceras (*Durnovarites*) *baueri* Collignon (1963: 159, pl. 305 (fig. 1311)) differs from *M. (D.) collignoni* sp. nov. in its coarse ribbing, depressed whorls, wide umbilicus and prominent umbilical tubercles. Its body chamber ornament is not known. *Mortoniceras* (*Durnovarites*) *rerati* Collignon (1963: 162, pl. 307 (figs 1312–1313)) differs from the Angolan material in much the same respects, but does not have the swollen umbilical tubercles of *M. (D.) baueri*. It very closely approaches *M. (D.) ishiaguense*.

Mortoniceras (*Durnovarites*) *subdepressum* Collignon (*in* Besairie 1936: 196, pl. 21 (figs 4–5)) is based upon a unique fragment with a very depressed whorl section. It was said to differ from *M. (D.) depressum* in having straighter ribs which are not projected forwards on the venter. It is more coarsely ribbed with a more depressed whorl section than *M. (D.) collignoni*.

Occurrence

Mortoniceras (*Durnovarites*) *collignoni* is known only from the uppermost Albian of Angola.

Subgenus *Angolaites* Spath, 1932

Type species *Subschloenbachia gregoryi* Spath, 1922

Discussion

Angolaites was separated as a subgenus of *Mortoniceras* (Spath 1932: 380) for ‘. . . serpenticones, with single costation from a very early stage, and two peripheral tubercles, close together’. The characters of the subgenus are consistent, making it an easily recognized and useful taxon.

Amongst mortoniceratinids, only *Drakeoceras* Young, 1957, and *Cantabrigites* Spath, 1933, have the same closely spaced ventrolateral tubercles whilst also lacking flank tubercles. *Drakeoceras* appears, however, to be a *Goodhallites* derivative characterized by its much narrower umbilicus and high whorls. The micromorph *Cantabrigites* is a contemporaneous form, abundant in western Europe where *Angolaites* is unknown, while the extreme rarity of *Cantabrigites* in Angola makes it unlikely that they represent sexual dimorphs.

Mortoniceras (*Angolaites*) *gregoryi* (Spath, 1922)

Figs 39G, 71, 72C, 73D

Subschloenbachia gregoryi Spath, 1922: 127, pl. 3 (fig. 1).

Mortoniceras (*Angolaites*) *gregoryi* (Spath) Reyment, 1955: 37, pl. 4 (fig. 13), pl. 6 (fig. 3).

Material

Three specimens, SAM-PCA3110, 3145 and 3235, from Praia-Egito, together with seven specimens from the Quissama Ridge of Cabo Ledo, SAM-PCA4601, 4608, 4611, 4626, 4685, 4712, and 4813, all preserved as composite internal moulds.

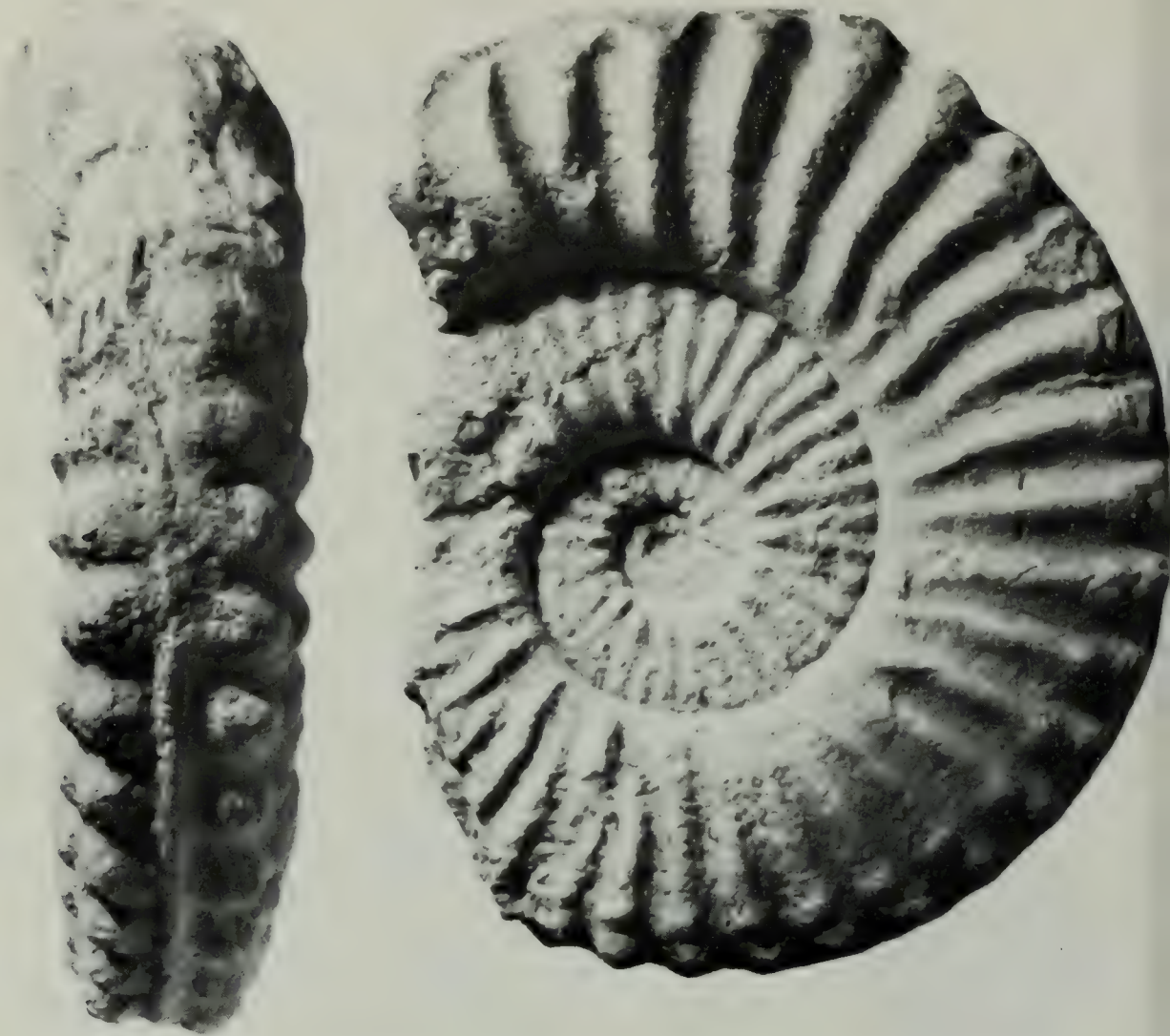


Fig. 71. *Mortonicerias* (*Angolaites*) *gregoryi* (Spath). The holotype, from the uppermost Albian at Catumbella, BMNH C20066. $\times 1$.

Description

The shell is very evolute, compressed, with a wide, shallow umbilicus (42–47% of the diameter). The umbilical walls are gently rounded and the flanks are slightly convex intercostally, converging somewhat towards the venter, with greatest width slightly above the umbilical shoulder.

Ribs begin very weakly on the umbilical wall and pass radially outwards to the umbilical shoulder where they terminate in fairly prominent bullae, about seventeen per whorl. Each bulla gives rise to one to two flank ribs, with frequent intercalatories which become more abundant in maturity. Across the flanks the ribs are prorsiradiate and all are ornamented with closely spaced double ventrolateral tubercles. There are thirty-nine ventrolateral tubercles on the outer whorl, and the upper ventrolateral tubercles are spirally notched. The venter is moderately narrow, with shallow sulci on either side of the siphonal keel.

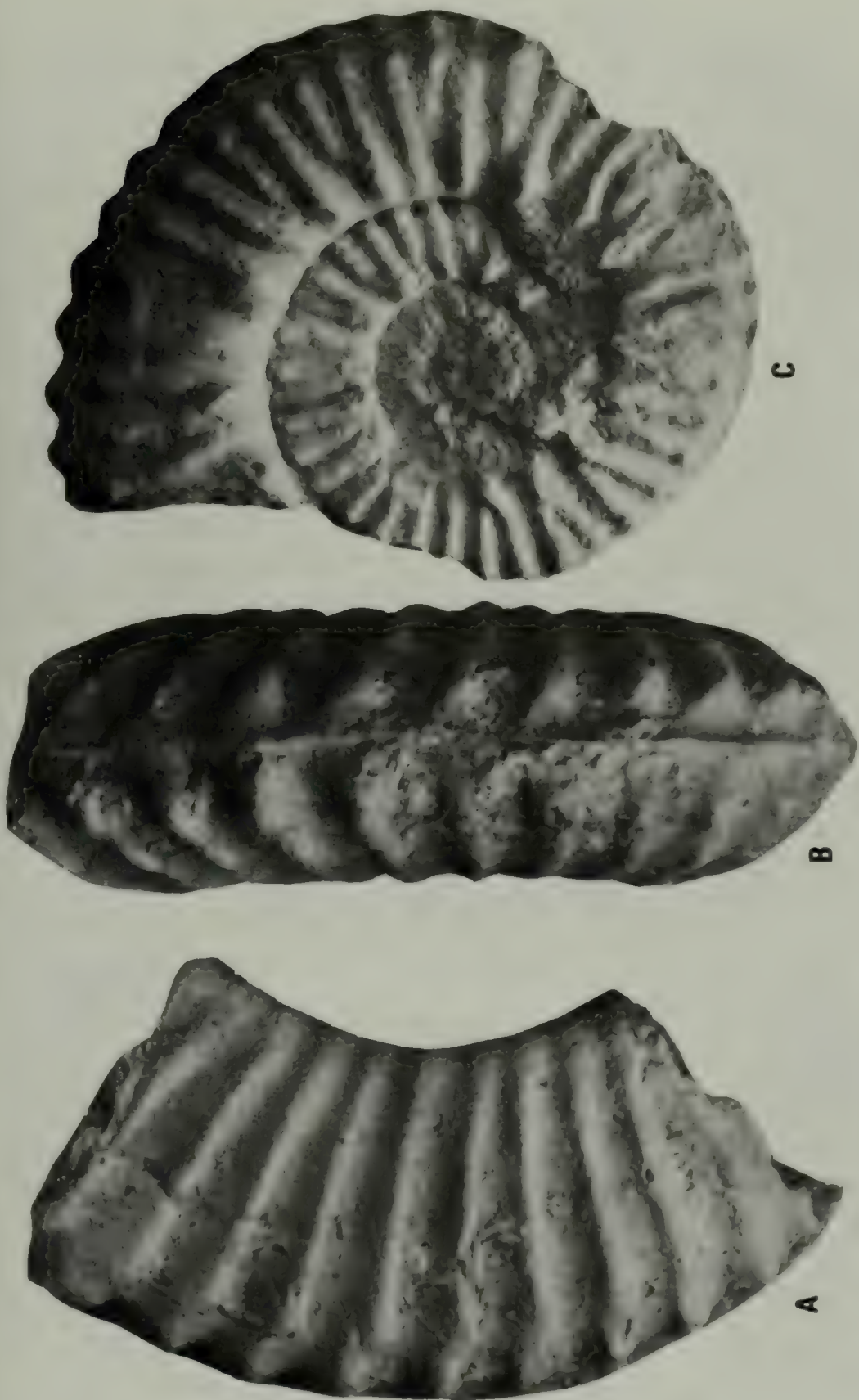


Fig. 72. A-B. *Mortonicerias* (*Angolaites*) *simplex* (Choffat). Lateral and ventral views of SAM-PCA3200. C. *Mortonicerias* (*Angolaites*) *gregoryi* (Spath). Lateral view of SAM-PCA3145. $\times 1$.



Fig. 73. A-C. *Mortonicerias* (*Angolaites*) *simplex* (Choffat). A. Lateral view of SAM-PCA3142. B. Lateral view of SAM-PCA3153. C. Lateral view of SAM-PCA3114. D. *Mortonicerias* (*Angolaites*) *gregoryi* (Spath). Lateral view of SAM-PCA3147. A $\times 0,66$, B-D $\times 1$.

Measurements

No.	D	H	W	w/H	U
SAM-PCA3145	85	25(29)	20(24)	0,8	40(47)
„	58	18(31)	—(—)	—	27(47)
SAM-PCA3235	67	22(32)	20(30)	0,9	28(42)

Discussion

Mortonicerias (Angolaites) gregoryi differs from *M. (A.) simplex* (Choffat) and *M. (A.) vicina* (Haas) in the common occurrence of bifurcating and intercalated ribs, and in having far fewer umbilical bullae.

Occurrence

Mortonicerias (Angolaites) gregoryi is known with certainty only from the Upper Albian of Angola and Nigeria.

Mortonicerias (Angolaites) simplex (Choffat, 1905)

Figs 3A–D, 54G–H, 72A–B, 73A–C, 74–77

Schloenbachia simplex Choffat, 1905: 35, pl. 4 (fig. 3).

Pervinquieria simplex var. *tenuis* Haas, 1942: 81, pl. 16 (fig. 1), figs 7e, 8a.

Inflaticerias sp. n. aff. *gregoryi* Spath, 1922: 127, pl. 3 (fig. 2).

Pervinquieria vicina Haas, 1942: 82, pl. 16 (fig. 2), fig. 8b.

Pervinquieria vicina var. *evoluta* Haas, 1942: 83, pl. 16 (fig. 3), fig. 8c.

Material

9 specimens, SAM-PCA3107, 3116, 3142, 3146, 3150, 3153, 3166, 3200 and 3249, from Praia-Egito, together with 30 specimens from the Quissama Ridge at Cabo Ledo, SAM-PCA4575, 4578–79, 4581–82, 4584–85, 4588, 4590, 4593–94, 4596, 4605, 4609, 4613, 4615–16, 4618, 4628, 4631, 4640, 4718, 4756, 4770, 4774, 4863, 4867–69, and 4874, all preserved as composite internal moulds.

Description

This species is abundant at Egito, with adult specimens attaining a diameter of 170 mm (SAM-PCA3142).

The shell is evolute, compressed, with the outer whorls only covering the preceding whorls to the top of the lower ventrolateral tubercles. The umbilicus is shallow and wide (41–47% of the diameter), with steep umbilical walls and well-rounded umbilical shoulders.

Ribbing begins at the umbilical seam, is rather faint at first, strengthening as it passes radially outwards to the umbilical shoulder. The ribs may strengthen slightly on the umbilical shoulder, but true umbilical tubercles are absent. In the immature growth stages, the flank ribs are slightly sinuous but on the final whorl they become adorally concave. Rare intercalated ribs occur only during the very early ontogenetic stages, and there are about twenty ribs per whorl. Lateral tubercles are lacking, but all ribs are ornamented with closely spaced double



Fig. 74. A-B. *Mortonicerias (Angolaites) simplex* (Choffat). Ventral and lateral views of SAM-PCA3116. C-D. *Mortonicerias (Angolaites) cf. simplex* (Choffat). Lateral and ventral views of SAM-PCA3179. $\times 1$.

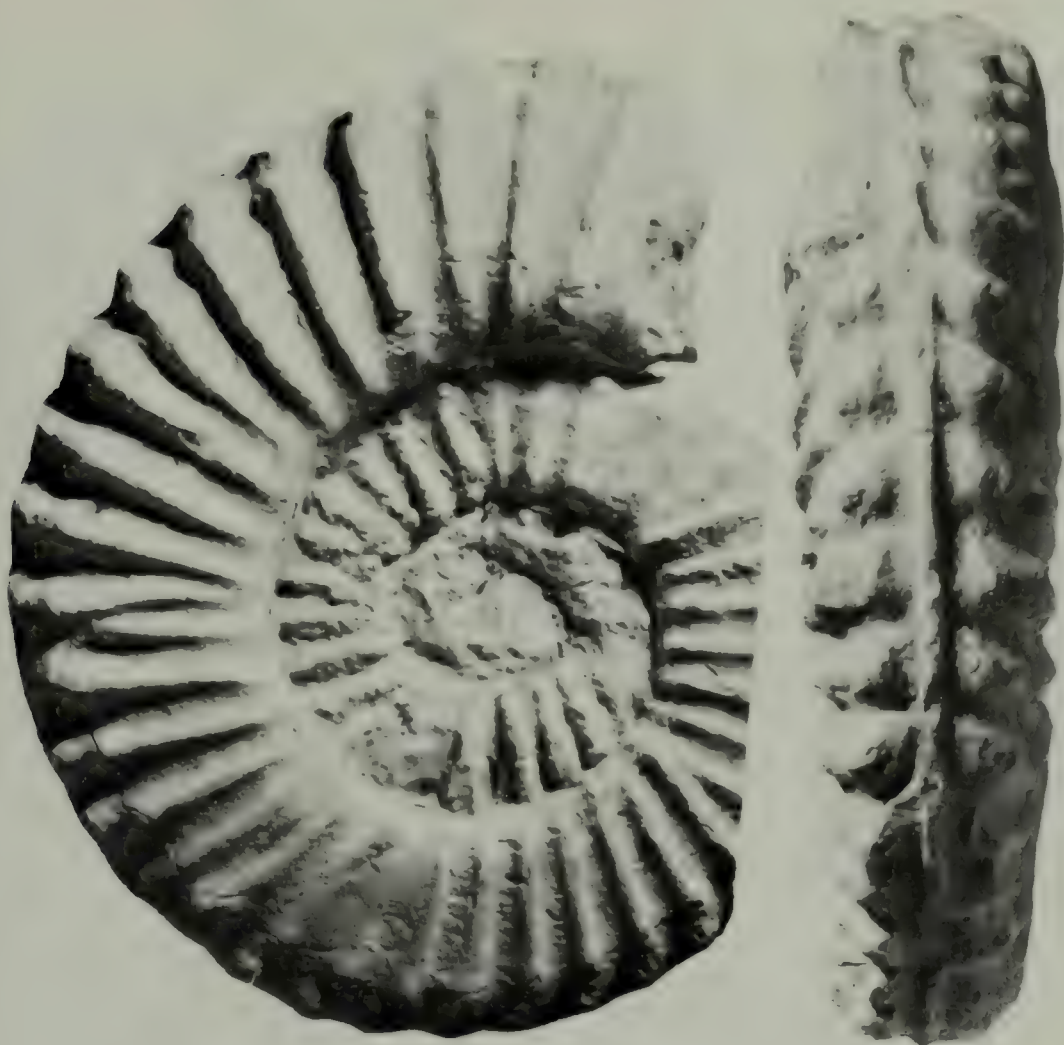


Fig. 75. *Mortonicerias (Angolaites) vicina* (Haas). The holotype BMNH-C20067. $\times 1$.

ventrolateral tubercles which are spirally notched, especially the upper ventrolateral tubercle. The narrow, rounded venter is keeled, with smooth sulci on either side. At large growth stages, the ventrolateral tubercles stand somewhat above the level of the keel.

Measurements

No.	D	H	W	W/H	U
SAM-PCA3142	173	48(28)	41(24)	0,85	81(47)
„	135	45(33)	35(26)	0,77	56(41)
SAM-PCA3107	91	31(34)	24(26)	0,77	37(41)
SAM-PCA3200	—	43(—)	33(—)	0,76	—
SAM-PCA3249	—	33(—)	26(—)	0,78	—
SAM-PCA3150	—	39(—)	35(—)	0,89	—
SAM-PCA3153	—	22(—)	19(—)	0,86	—
SAM-PCA3146	—	31(—)	26(—)	0,84	—

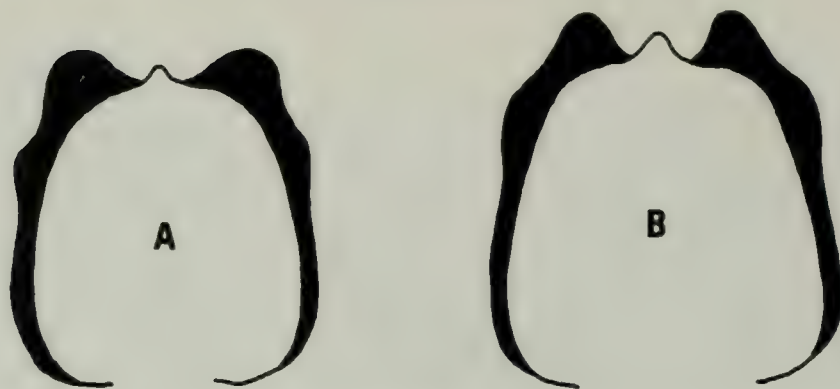


Fig. 76. *Mortonicerias (Angolaites) simplex* (Choffat). Whorl sections. A. SAM-PCA3166. B. SAM-PCA3116. $\times 1$.

Discussion

Spath (1922) briefly discussed and figured a specimen which he considered to differ from *M. gregoryi* in having coarser, more distantly ribbed inner whorls (Fig. 75). This specimen was renamed *Pervinquieria vicina* by Haas (1942); it is in the British Museum (BMNH C20067) and, so far as the writers are able to judge, differs from *M. (A.) simplex* only in its coarser, more distant ribbing with five ribs in a distance equal to the whorl height, whereas in *M. (A.) simplex* there are eight to nine. The differences are slight, and within the range of variation seen in *M. (A.) simplex* from Egito; they are not regarded as of specific significance.

Occurrence

Mortonicerias (Angolaites) simplex is known only from Angola.

Genus *Cantabrigites* Spath, 1933

Type species *Mortonicerias (Cantabrigites) cantabrigense* Spath;
by original designation

Discussion

The first appearance of the name *Cantabrigites* Spath (1932: 380) was as a *nomen nudum*, the diagnosis and description of the type species appearing only a year later (Spath 1933: 436). Consequently, the valid date of introduction for *Cantabrigites* is 1933.

Spath (1933) proposed *Cantabrigites* as a subgenus of *Mortonicerias* for 'dwarf-forms with reduced, generally single and almost untuberculate costation and greatly simplified suture-line'. In maturity, many typical *Mortonicerias* commonly exceed 200–300 mm in diameter, whereas *Cantabrigites* is mature at diameters of less than 80 mm. It would appear, therefore, to be a genuine micromorph taxon. The fact that *Cantabrigites* is restricted to one level in the Upper Albian, viz. the *dispar* Zone, suggests that it is not the microconch of *Mortonicerias*. *Cantabrigites* differs so greatly from *Mortonicerias vespertinum* (Morton), the type of the genus, that the authors consider the differences sufficient for generic separation.

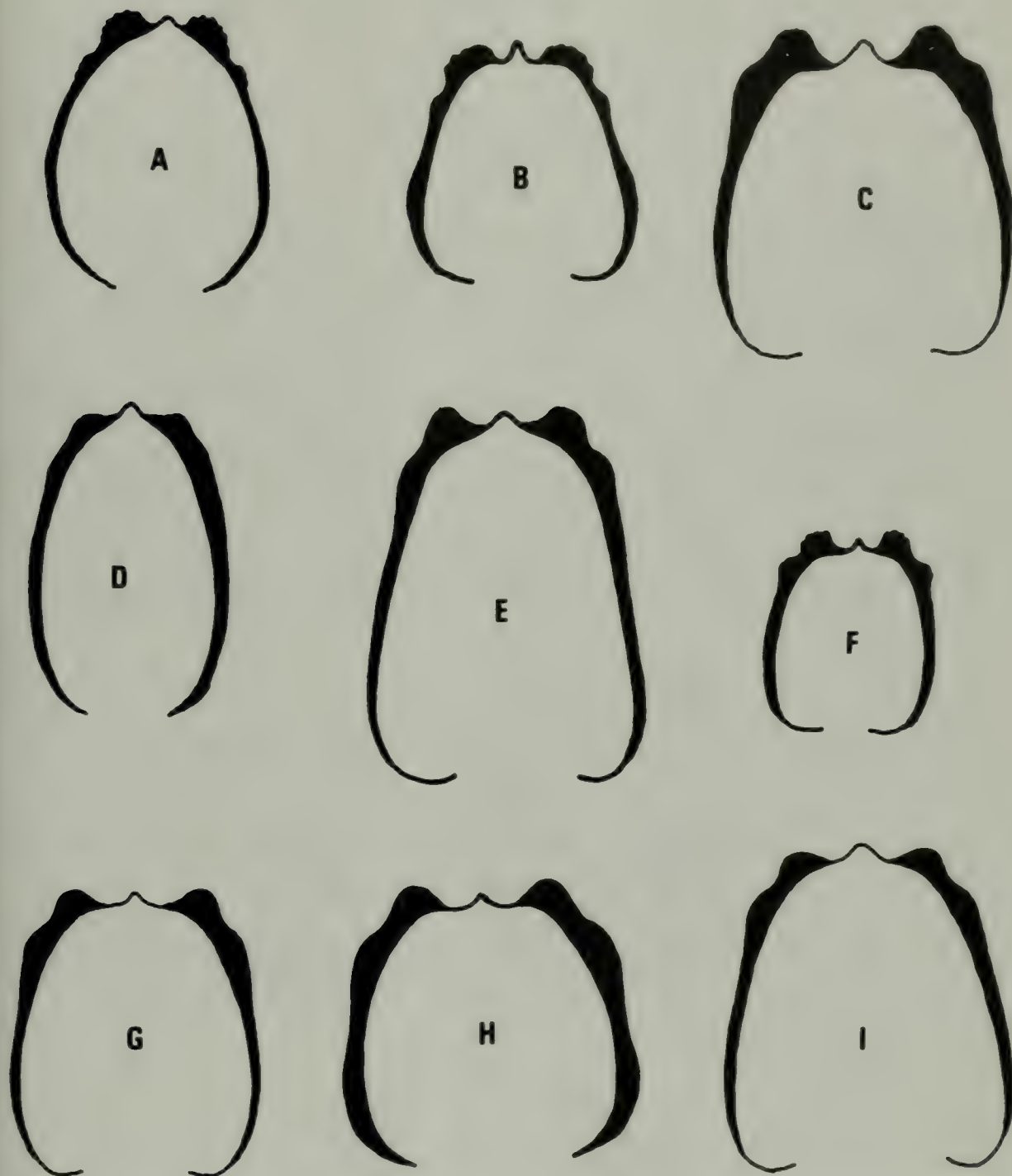


Fig. 77. *Mortonicerias (Angolaites) simplex* (Choffat). Whorl sections. A. SAM-PCA3249. B. SAM-PCA3147. C. SAM-PCA3150. D. SAM-PCA3144. E. SAM-PCA3200. F. SAM-PCA3153. G. SAM-PCA3111. H. SAM-PCA3179. I. SAM-PCA3200. $\times 1$.

Cantabrigites? curvatum Renz, 1968

Figs 78–79

Cantabrigites curvatum Renz, 1968: 61, pl. 11 (figs 1a–b, 2a–c), figs 20g, 21f.*Material*

A single specimen, SAM-PCA3177, from a horizon some way below the main occurrence of *Stoliczkaia* at Egito, in road gravels.

Description

The shell is evolute, with a wide, moderately deep umbilicus and a slightly compressed, subquadrate intercostal whorl section. The umbilical shoulders are well rounded and the flanks convex, with maximum width at about midflank. Ribs begin at the umbilical seam and pass radially outwards to small, but distinct, bullae on the umbilical shoulder. The ribs are rather thick, robust, and vary from slightly rursiradiate to slightly prorsiradiate across the flanks. Where no umbilical bullae are present, some ribs are intercalated at the level of the umbilical shoulder, so that there are eleven ribs per half whorl, of which six arise from umbilical bullae. Each rib is ornamented with a prominent, obliquely clavate, ventrolateral horn which projects backwards. There appears to be the faintest swelling just below the ventrolateral horns which may represent a very weakly developed lower ventrolateral tubercle. There is a distinct siphonal keel.

Measurements

No.	D	H	W	W/H	U
SAM-PCA3177	29	11(38)	9(31)	0,82	13(41)

Discussion

The Angolan specimen is indistinguishable from the holotype from Ste Croix, Switzerland, although the writers are in some doubt as to the generic identity of this species, since it closely resembles some of the earlier *Neokentroceras* spp. known from Angola. As, however, this species is known only from three small specimens and *Neokentroceras* is typical of the low Upper Albian of Angola and Nigeria, tentative assignment to *Cantabrigites* seems preferable, it being an homoeomorphous development only.

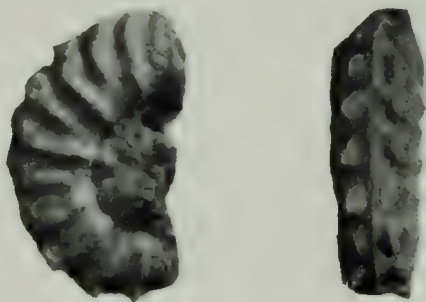


Fig. 78. *Cantabrigites? curvatum* Renz. Lateral and ventral views of SAM-PCA3177. $\times 1$.



Fig. 79. *Cantabrigites? curvatum* Renz. Whorl section of SAM-PCA3177. $\times 2$.

Mortoniceras (*Durnovarites*) *neokentroides* Wiedmann & Dieni (1968: 146, pl. 13 (fig. 5)) was, as its specific name implies, considered to resemble *Neokentroceras*. It differs from the present species in having well-developed upper and lower ventrolateral tubercles which are elongated at right angles to the keel.

Mortoniceras? nanum Spath (1933: 411, pl. 43 (fig. 6), pl. 46 (figs 4-5), fig. 141) (Fig. 80) resembles the present species, but has double ventrolateral tubercles and lacks the posteriorly directed horns of *C? curvatum*.

Occurrence

Cantabrigites? curvatum Renz is known only from Switzerland and Angola.

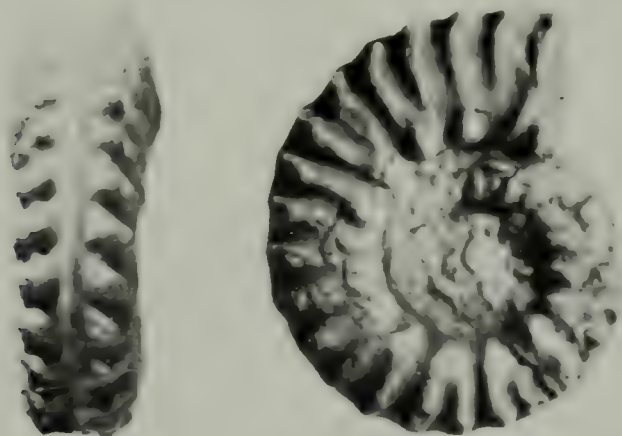


Fig. 80. *Mortoniceras? nanum* Spath. The holotype, BMNH-C72726, from the Cambridge Greensand. $\times 1$.

Genus *Drakeoceras* Young, 1957

Type species *Drakeoceras drakei* Young, 1957

Discussion

Young (1957) erected the new genus *Drakeoceras* for *Goodhallites*-like forms in which the ventrolateral tubercles are doubled. As such, therefore, *Drakeoceras* bears the same relationship to *Goodhallites* that *Angolaites* does to

Mortoniceras, and further work may show that it is best treated as a subgenus of *Goodhallites*. *Drakeoceras* differs from *M. (Angolaites)* in being higher whorled, with *Goodhallites*-like inner whorls and a more quadrate whorl section in maturity, as well as retaining prominent umbilical bullae and bifurcating ribs onto the body chamber.

Drakeoceras cf. *dellense* Young, 1957

Figs 3E-F, 81-82

Compare

Drakeoceras dellense Young 1957: 25, pl. 7 (fig. 1), pl. 10 (figs 4-5, 8-10), figs 2j, 3a, h-j.

Material

Six specimens, SAM-PCA4662, 4673, 4705, 4733, 4786, and 4800, from the Quissama Ridge at Cabo Ledo, all poorly preserved limestone steinkerns, appear to belong here.

Description

The shell is strongly compressed and moderately involute (umbilicus 23-25% of the diameter). The umbilicus is fairly narrow and shallow, with steep umbilical walls and evenly rounded umbilical shoulder. The broad flanks are slightly convex and converge towards the narrowly arched venter. The whorl section is compressed, elliptical ($w/h = 0,70-0,94$).

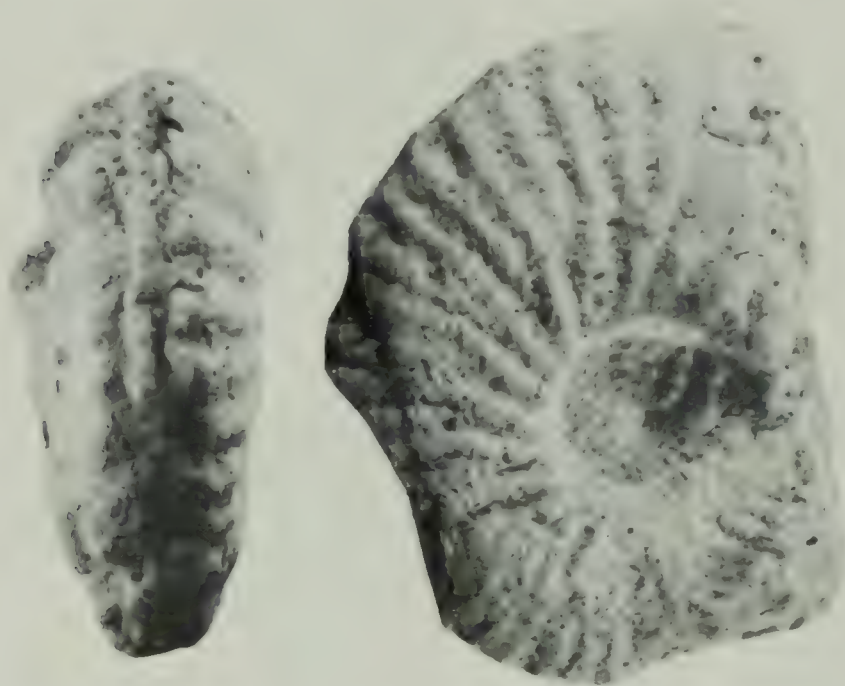


Fig. 81. *Drakeoceras* cf. *dellense* Young. Ventral and lateral views of SAM-PCA4800. $\times 1$.

Ornament comprises about twelve weak umbilical bullae per half-whorl, from which ribs commonly arise in pairs, or singly with an intercalated rib between long ribs. The ribs are initially strongly prorsiradiate, but recurve just below midflank. The ribs are broader than the interspaces and there are about twenty-four per half-whorl at the venter. All ribs are ornamented with very weak (? due to abrasion) lower and distinct upper ventrolateral tubercles. There is a prominent siphonal keel.

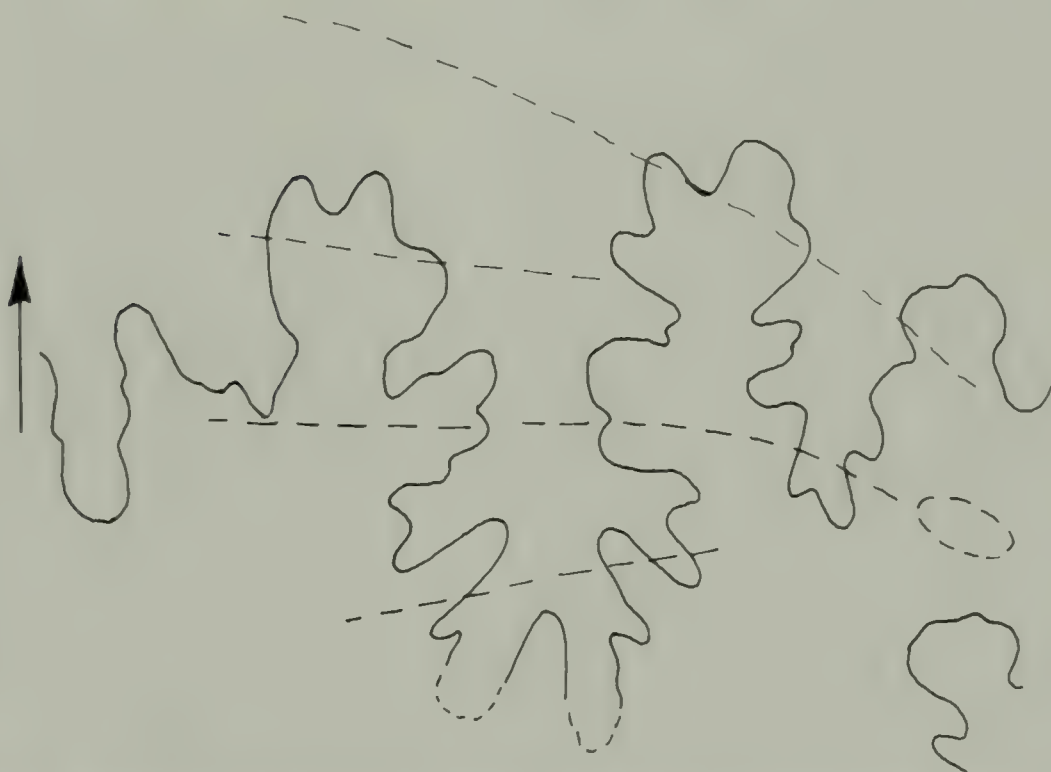


Fig. 82. *Drakeoceras* cf. *dellense* Young. Eroded suture at 65 mm diameter. Approx. $\times 3$.

Discussion

The Angolan specimen is closest to *D. dellense* from which it differs only in being somewhat more involute. It is significant that in Texas *D. dellense* is associated with *M. (Durnovarites) perinflatum* (Spath) (= *D. adkinsi* Young) and is probably, therefore, strictly contemporaneous with the Angolan specimens. Differences from other species of *Drakeoceras* are noted by Young (1957).

Occurrence

Drakeoceras dellense is currently known only from the *dispar* Zone of Texas and probably Angola.

Family *Binneyitidae* Reeside, 1927Genus *Borissiakoceras* Arkhangel'skii, 1916Type species *Borissiakoceras mirabile* Arkhangel'skii, 1916*Discussion*

As currently diagnosed (Wright *in* Arkell *et al.*, 1957), the Binneyitidae is a family of micromorph ammonites characterized by their compressed, flat-sided form, narrow umbilicus and greatly simplified suture. Considered to be descended from the typically Middle Albian *Falciferella*, the earliest recorded binneyitids are from the Middle Cenomanian of the Western Interior (Cobban 1961), although we know of specimens of comparable age from western Europe (Kennedy & Juignet 1973) and Zululand. The time separating the last appearance of *Falciferella* and the first appearance of *Borissiakoceras* has been something of a problem in this phylogenetic scheme. However, Brunnschweiler (1959) has recorded species of '*Falciferella*' from the late Albian of Australia which appear to bridge this gap. Our present record of *Borissiakoceras* from the uppermost Albian of Angola closes the gap even further, and, by extending the record of *Borissiakoceras* as far back as the late Albian, provides a direct morphological, chronological and phylogenetic link with the Middle Albian *Falciferella*. Cobban (1961: 747) diagnosed *Borissiakoceras* as follows: 'This genus is characterized by the small size of the conchs which are ordinarily compressed and moderately evolute to somewhat involute. The venter is rounded to flat. Most shells are smooth but a few have raised falcoid growth lines or faint closely spaced falcoid ribs. Nodes, when present, are on the ventrolateral shoulder. The suture has a broad ventral lobe indented by a broad, shallow ventral saddle. The first lateral saddle is bifid and as wide as the ventral lobe. The first lateral lobe is narrow, bifid, and about half as wide as the ventral lobe. The second lateral saddle is trifid and higher and broader than the first. The second lateral lobe is about half as large as the first and tends to be bifid. The auxiliaries, which are small and shallow, may be divided into bifid lobes and saddles.'

Casey (1954: 27) introduced *Falciferella* (type species: *F. milbournei* Casey, 1954: 274, pl. 7 (figs 1-5), fig. 3) as follows: 'Micromorph platycones with narrow, sharp-rimmed umbilicus and tabulate venter, feebly carinate in early youth. Test with strongly falcoid lineation or sub-costation, and a faint spiral groove at the middle of the sides. Mouth border plain. Suture-line of simplified *Aconeceras* pattern, with reduced auxiliary elements.'

In southern England, *Falciferella* is known only from the Middle Albian *Euhoplites loricatus* Zone (*intermedius* and *niobe* Subzones) (Owen 1971), although Brunnschweiler (1959) has recorded two species from the Upper Albian of Australia. *Falciferella breadeni* Brunnschweiler (1959: 15, pl. 1 (figs 5-6)) is associated with *Labeceras* and *Myloceras* and is thus of early late Albian age. In this species, the earliest whorls are smooth, but strong falcate ribs develop in maturity and form weak folds across the tabulate venter. The suture-line of

F. breadeni is simpler than in *F. milbournei*, in which respect it is closer to *Borissiakoceras*. It differs, however, in the trifid nature of the first lateral lobe, but there is a tendency towards trifurcation of this sutural element in *B. orbiculatum* Stephenson (cf. Cobban 1961, fig. 5a, f). Although a trifid first lateral lobe is known in *Falciferella*, the characters of *F. breadeni* are largely those of *Borissiakoceras*, and it is to the latter genus that we refer '*F.*' *breadeni* and '*F.*' *reymenti*.

Borissiakoceras sp. nov. ? aff. *reymenti* (Brunnschweiler, 1959)

Fig. 31H-I

Compare

Falciferella reymenti Brunnschweiler 1959: 15, pl. 1 (figs 5-6).

Material

A single specimen, USNMNH 236980, with recrystallized shell preserved from Porto Amboim.

Description

Shell small, compressed (in part due to post-mortem deformation), with broad, flat flanks and a narrowly rounded venter. In places the venter appears to be fastigiate, but this is probably due to secondary crushing. The umbilicus is narrow (23% of the diameter) and the shell smooth.

Measurements

No.	D	H	W	W/H	U
USNMNH 236980	17	$\pm 7,3(43)$	$\pm 3(18)$	0,41	4(23)

Discussion

The only other species of *Borissiakoceras* yet known from late Albian strata are *B. breadeni* (Brunnschweiler) (1959: 15, pl. 1 (figs 5-6)) and *B. reymenti* (Brunnschweiler) (1959: 16, pl. 1 (figs 7-8)) from the Oodnadatta region of South Australia. Both these species differ from the Angolan specimen in their much narrower umbilicus (13-14% of diameter) and in possessing rather prominent falcate ribs. Cobban (1961) has shown, however, that the latter feature is not consistently developed, even within a single *Borissiakoceras* population, with both ribbed and smooth variants occurring side by side. Consequently differences in ornament of this type may not be of specific importance.

Smooth variants of *Borissiakoceras orbiculatum* Stephenson (1955: 64, pl. 6 (figs 1-4)) closely resemble the present specimen, but are much younger (Middle Cenomanian). *Borissiakoceras compressum* Cobban (1961: 747, pl. 87 (figs 19-33), pl. 89 (figs 1-9), fig. 4a-k) also resembles the present species, but is of Middle Cenomanian age and has a narrower umbilicus (14-17% of the diameter). *Borissiakoceras mirabile* Arkhangel'skii (1916: 55, pl. 8 (figs 2-3))

differs from the Angolan example in its much wider umbilicus (37% of the diameter) as well as being a Lower Turonian species. *Borissiakoceras reesidei* Morrow (1935: 463, pl. 49 (fig. 7), pl. 50 (fig. 5), fig. 8) is an Upper Cenomanian species which, like *B. orbiculatum*, cannot be separated from the unique Angolan example without knowledge of the suture-line characteristics of the latter.

Occurrence

Upper Albian of Angola; species with which the specimen is compared came from the Upper Albian of Australia.

AGE OF THE FAUNA

At present there are certain problems concerning the scope and nomenclature of the *Stoliczkaia dispar* Zone and its subzones. The divisions of the Albian Stage in England were erected by Spath on the basis of his understanding of the successions at Folkestone and elsewhere in England, and are based on firm stratigraphic principles. Spath (1943) gave the following zonation through the Upper Albian of southern England:

<i>Stoliczkaia dispar</i> Zone	{	<i>Stoliczkaia dispar</i> / <i>Durnovarites perinflatum</i> Subzone
	{	<i>Arrhaphoceras substuderi</i> Subzone
	{	<i>Mortoniceras aequatoriale</i> Subzone
<i>Mortoniceras inflatum</i> Zone	{	<i>Callihoplites auritus</i> Subzone
	{	<i>Hysterocheras varicosum</i> Subzone
	{	<i>Hysterocheras orbigny</i> Subzone

Whilst accepting Spath's subdivision of the *S. dispar* Zone, Breistroffer (1940) showed that *Arrhaphoceras substuderi* (Spath) was common to both the *perinflatum*/*dispar* and *substuderi* Subzones and was, therefore, unsuitable for use as a subzonal index. Instead, he recognized a lower subzone of *S. (Faraudiella) gardonica*—*S. (F.) rhamnonota*—*Mariella gresslyi*—*Turrilitoides toucasi*. By 1947, however, Breistroffer had realized that *S. (F.) gardonica* and *S. (F.) rhamnonota* were synonyms of *S. (F.) blancheti* (Pictet & Campiche) and consequently renamed Spath's *A. substuderi* Subzone the 'Zone á *Paraturrilites Gresslyi*, *Turrilitoides Hugardianus* et *Stoliczkaia (Faraudiella) Blancheti*'. The upper horizon (Spath's *dispar*/*perinflatum* Subzone) was referred to a 'Zone á *Pervinqueria (Durnovarites) perinflata*, *P. (Subschloenbachia) rostrata*, *Paraturrilites Bergeri* et *Stoliczkaia dispar*'.

On the basis of newly exposed sections, however, Owen (1976) has recently shown that Spath's *aequatoriale* Subzone is a remanié assemblage which cannot be distinguished from the underlying subzone of *Callihoplites auritus* and he has, therefore, proposed its abandonment. In addition, Owen (1976) recalled Breistroffer's (1940) observation that *Arrhaphoceras substuderi* was unsuitable for use as a subzonal index in the *S. dispar* Zone and, because Owen (1976: 492) quite inexplicably considered *S. (F.) blancheti* '... is not sufficiently distinct to

be used as a subzonal index', he proposed to replace this subzonal index with *Mortoniceras rostratum* (J. Sowerby). This, however, is a very unfortunate suggestion because *M. rostratum* was for many years (because of misidentification) the index species for the earlier zone now called after *M. inflatum*. In addition, Breistroffer (1947) has subsequently used it as one of the subzonal indices for Spath's *dispar/perinflatum* Subzone. Moreover, it is abundantly clear that the true characters of *M. rostratum* are not known since all the material assigned by Spath (1932, pl. 38 (fig. 4), pl. 39 (fig. 4), pl. 40 (figs 1, 7), pl. 41 (fig. 7)) to this species was renamed *Pervinqueria fallax* by Breistroffer (1940: 67). Thus, only Sowerby's holotype (Fig. 70), now in the Oxford University Museum, is without doubt assignable to this species. The authors' have had the opportunity of studying the holotype of *M. rostratum*. Its inner whorls are obscured by matrix whilst the ribs of the body chamber bear four rows of tubercles. Although a number of species of *Mortoniceras* s.s. have four rows of tubercles on the inner whorls, the upper and lower ventrolateral tubercles coalesce on the body chamber of *M. (Mortoniceras)* to produce ventrolateral horns and thus only three rows of tubercles remain on the body chamber. In the writers' opinion, therefore, *M. rostratum* is a species of *Durnovarites*, a subgenus so far recorded only from Spath's *dispar/perinflatum* Subzone, and is unsuited, therefore, for use as the subzonal index of the lower part of the *S. dispar* Zone. Moreover, since Owen (1976) does not state what he takes to represent *M. rostratum*, the species to which he is referring is totally unrecognizable. For this reason, the writers would propose a simple return to Breistroffer's (1947) subdivision of the *S. dispar* Zone into a lower subzone of *S. (F.) blancheti*, immediately overlying the *Callihoplites auritus* Subzone, and an upper subzone of *M. (Durnovarites) perinflatum*.

With the possible exception of the lower horizon at Egito, the present faunas can be referred with confidence to the *M. (D.) perinflatum* Subzone on the basis of the presence of *S. (Stoliczkaia)*, *M. (Durnovarites)* and the heteromorphs present. There does, however, seem to be some compositional difference in the faunas. Thus, at Praia-Egito the fauna comprises:*

Anisoceras perarmatum Pictet & Campiche

A. armatum (J. Sowerby)

A. haasi sp. nov.

A. phillipsi sp. nov.

A. cf. arrogans (Giebel)

A. aff. exoticum Spath

A. aff. subarcuatum Spath

A. aff. spathi (Wiedmann)

Hamites virgulatus Brongniart

H. duplicatus Pictet & Campiche

Puzosia cf. *sharpei* Spath

Desmoceras latidorsatum perinflatum subsp. nov.

* These lists on pp. 299-301 follow the order in the text. Ed.

Stoliczkaia tenuis Renz
Mortoniceras (Durnovarites) collignoni sp. nov.
M. (Angolaites) simplex (Choffat)
M. (A.) gregoryi (Spath)

A somewhat lower level at this locality has yielded:

Tetragonites kitchini (Krenkel)
Mariella gresslyi (Pictet & Campiche)
Cantabrigites? curvatum Renz

The fauna from Cabo Ledo includes the following species:

Anisoceras perarmatum Pictet & Campiche
A. armatum (J. Sowerby)
A. phillipsi sp. nov.
Idiohamites dorsetensis Spath
Hamites virgulatus Brongniart
Mariella cf. *oehlerti* (Pervinquière)
Stoliczkaia sp.
Mortoniceras (Durnovarites) perinflatum (Spath)
M. (Angolaites) simplex (Choffat)
M. (Angolaites) gregoryi (Spath)
M. (Mortoniceras) spp.
Drakeoceras cf. *dellense* Young

This fauna differs from the higher horizon at Praia-Egito in that *M. (Mortoniceras)* is still fairly abundant whilst *M. (Durnovarites)* is rather rare. This suggests that the Cabo Ledo fauna may be somewhat older than the upper horizon at Praia-Egito, although the possibility of mixing of different horizons cannot be wholly dismissed.

The fauna from Porto Amboim comprises:

Phylloceras (Hypophylloceras) seresitense Pervinquière
Tetragonites collignoni Breistroffer
T. jurinianus (Pictet)
Eogaudryceras italicum Wiedmann & Dieni
Anisoceras perarmatum Pictet & Campiche
A. armatum (J. Sowerby)
A. haasi sp. nov.
Idiohamites dorsetensis Spath
I. cf. elegantulus Spath
I. pygmaeus sp. nov.
Hamites virgulatus Brongniart
Mariella circumtaeniatus (Kossmat)
Desmoceras latidorsatum perinflatum subsp. nov.
Stoliczkaia tenuis Renz

Mortoniceras (Durnovarites) perinflatum (Spath)

M. (D.) subquadratum Spath

M. (Angolaites) simplex (Choffat)

Hysterocheras? cf. *ootaturense* (Stoliczka)

Borissiakoceras sp. nov? aff. *reymonti* (Brunnschweiler)

The abundance of very compressed *Stoliczkaia* at Porto Amboim, together with the relative rarity of mortoniceratinids, suggests that this fauna may be somewhat younger than the upper horizon at Praia-Egito, although stratigraphic evidence for this is lacking. None the less, the *Stoliczkaia* fauna from here bears a very close resemblance to the 'Submantelliceras'—*Utaturiceras* assemblages that characterize the basal Cenomanian of many regions, although the persistence of *Mortoniceras* at this level suggests that it is still best regarded as uppermost Albian.

When the composition of the Angolan faunas is considered, there are marked differences from the faunas of the European *perinflatum* subzone in addition to the obvious absence of hoplitids. Noticeable in the Angolan assemblage is the complete absence of the widely distributed *Mariella* of the *bergeri-miliaris* group, *Lechites*, *Stoliczkaia (Faraudiella)*, *Turrilitoides*, *Scaphites*, *Ostlingoceras* and nautiloids, together with the rarity of *Hamites* and *Cantabrigites*. Moreover, *Stoliczkaia tenuis* is rather different from the *S. dorsetensis*—*notha*—*dispar* plexus which characterizes the uppermost Albian of western Europe.

Although some differences may be ecological (in particular with respect to the heteromorphs and the absence of hoplitinids), it seems possible that two slightly different levels in the uppermost Albian are represented. It is perhaps noteworthy, therefore, that in Texas, *M. (D.) perinflatum* is known only from the Pawpaw Formation (Young 1957), some way below the basal Cenomanian faunas of the uppermost Main Street and Grayson/Del Rio sequences. It also occurs below the main level of *Stoliczkaia* in Poland (Marcinowski & Naidin 1976).

Notwithstanding these differences, the abundance of *Stoliczkaia*, together with *M. (Durnovarites) perinflatum* and *Anisoceras* of the *perarmatum* group, is sufficient to date the Porto Amboim fauna at *M. (D.) perinflatum* Subzone of the *S. dispar* Zone, and to point to the possibility of even further subzonal refinement of this critical interval.

SUMMARY

The Angolan littoral has yielded rich ammonite faunas referable to the uppermost Albian zone of *Stoliczkaia dispar*, and mainly to the upper subzone of *Mortoniceras (Durnovarites) perinflatum*. The following species are described:

Phylloceras (Hypophylloceras) seresitense Pervinqui re

Tetragonites (Tetragonites) collignoni Breistroffer

Tetragonites (Tetragonites) kitchini (Krenkel)

Tetragonites (*Tetragonites*) *jurinianus* (Pictet)
Eogaudryceras (*Eogaudryceras*) *italicum* Wiedmann & Dieni
Anisoceras (*Anisoceras*) *perarmatum* Pictet & Campiche
Anisoceras (*Anisoceras*) *armatum* (J. Sowerby)
Anisoceras (*Anisoceras*) *haasi* sp. nov.
Anisoceras (*Anisoceras*) *phillipsi* sp. nov.
Anisoceras (*Anisoceras*) cf. *arrogans* (Giebel)
Anisoceras (*Anisoceras*) aff. *subarcuatum* Spath
Anisoceras (*Anisoceras*) aff. *exoticum* Spath
Anisoceras (*Anisoceras*) cf. *spathi* (Wiedmann)
Idiohamites *dorsetensis* Spath
Idiohamites cf. *elegantulus* Spath
Idiohamites *pygmaeus* sp. nov.
Hamites *virgulatus* Brongniart
Hamites *duplicatus* Pictet & Campiche
Mariella (*Mariella*) *circumtaeniatus* (Kossmat)
Mariella (*Mariella*) *gresslyi* (Pictet & Campiche)
Mariella (*Mariella*) cf. *oehlerti* (Pervinquière)
Mariella (*Mariella*) *nobilis* (Jukes-Browne)
Puzosia (*Puzosia*) cf. *sharpei* Spath
Desmoceras (*Desmoceras*) *latidorsatum perinflatum* subsp. nov.
Stoliczkaia (*Stoliczkaia*) *tenuis* Renz
Hysterocheras ? cf. *ootaturense* (Stoliczka)
Mortoniceras (*Durnovarites*) *perinflatum* (Spath)
Mortoniceras (*Durnovarites*) *subquadratum* Spath
Mortoniceras (*Durnovarites*) *collignoni* sp. nov.
Mortoniceras (*Angolaites*) *simplex* (Choffat)
Mortoniceras (*Angolaites*) *gregoryi* (Spath)
Drakeoceras cf. *dellense* Young
Cantabrigites ? *curvatum* Renz
Borissiakoceras sp. nov. ? aff. *reymonti* (Brunnschweiler)

The majority of these species have not previously been described from Angola; although precisely correlated with the *perinflatum* Subzone, there are differences in composition when compared with European faunas. In part these reflect differences between biogeographic provinces (e.g. the sparsity or absence of some heteromorphs). Other differences suggest that it may be possible to further subdivide the *dispar* Zone and the fauna also permits discussion of recent reviews of Upper Albian zonation, especially by Owen (1976). A return to a twofold division of the *dispar* Zone into *Stoliczkaia* (*Faraudiella*) *blancheti* and *Mortoniceras* (*Durnovarites*) *perinflatum* Subzones is suggested.

The chief systematic conclusions from the paper are discussions of intra-specific variation in *Phylloceras* (*Hypophylloceras*), *T.* (*Tetragonites*), *D.* (*Desmoceras*), *E.* (*Eogaudryceras*) and *S.* (*Stoliczkaia*) species.

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6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierti Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text

e.g. '... the Figure depicting *C. namacolus* ...'; '... in *C. namacolus* (Fig. 10) ...'

(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names

e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene

(c) Scientific names, but not their vernacular derivatives

e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as

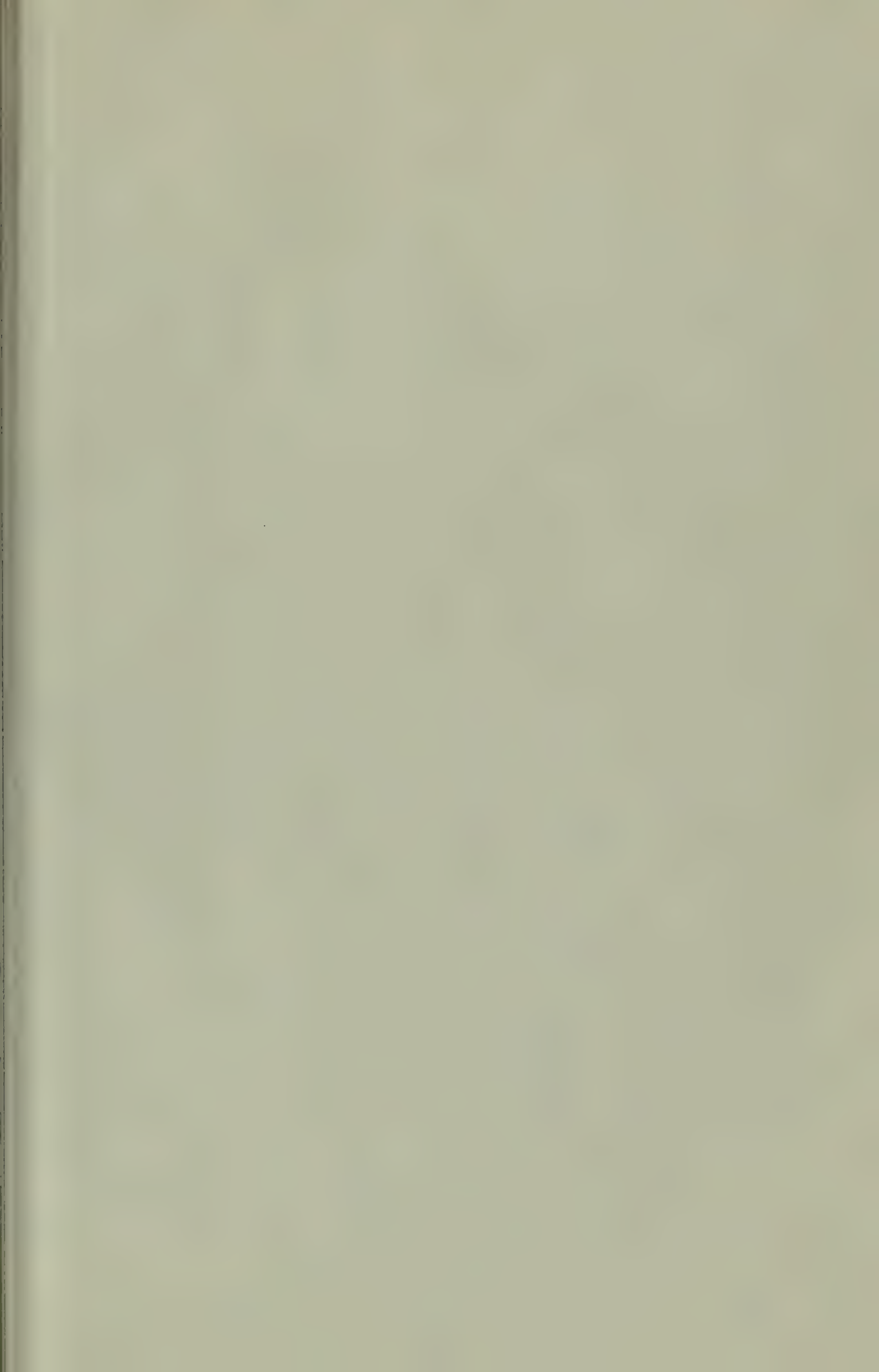
'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

M. R. COOPER
&
W. J. KENNEDY

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